



# The aquatic and wetland vegetation of Lake Doberdò: an analysis for conservation value assessment of a disappearing lake of the Classical Karst (North East Italy)

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## Abstract

Lake Doberdò (Classical Karst) is a well-known example of karst lakes, temporary lakes that seasonally fill and empty through springs and swallow holes connected to the underground waters. It is an area of exceptional interest for geological-geomorphological and biodiversity conservation, and is part of the Natura 2000 network. Its peculiar hydro-ecological nature allows an impressive variety of species and habitats. A phytosociological survey was carried out to provide a comprehensive analysis of the vegetation. On the basis of 177 phytosociological relevés and multivariate analysis 43 communities were found, belonging to *Platyhypnidio-Fontinalietea antipyreticae*, *Lemnetea minoris*, *Potametea pectinati*, *Bidentetea tripartitae*, *Isoëto-Nanojuncetea*, *Phragmito-Magnocaricetea*, *Agrostietea stoloniferae*, *Molinio-Arrhenatheretea*, *Filipendulo ulmariae-Convolvuletea sepium*, *Alnetea glutinosae*, *Rhamno catharticae-Prunetea spinosae*, *Alno glutinosae-Populetea albae*. The *Leucojo aestivi-Poetum pratensis* association including waterside periodically flooded meadows is validated. Compared to the past, various communities show a change in their distribution while some valuable coenoses were not found. 21 communities are attributed to 8 Annex I Habitats of the 92/43/EEC Directive. The study confirms the high value of Lake Doberdò for biodiversity conservation but highlights an ongoing process of environmental change due to both natural and human-related causes including modifications of the hydrological regime and abandonment of traditional agricultural practices. An overview of the features of Lake Doberdò is provided to compare this disappearing lake with the karst groundwater-dependent wetlands found in Ireland called “turloughs”, corresponding to Annex I Habitat 3180\*. Also on the basis of the current interpretation and distribution of this habitat type at the EU level, a proposal is presented to recognize and protect this outstanding area of the Natura 2000 network in Italy as the habitat 3180\*, modelled on Irish turloughs.

## Keywords

biodiversity conservation, Karst, phytosociology, temporary wetlands, turloughs, wetland habitats

## Introduction

The Karst plateau that extends behind Trieste across the border between SW Slovenia and NE Italy is known for its aridity and lack of surface water and is considered one of the best karst examples in the world (Ford and Williams 2007): indeed, the international scientific term “karst” adopted for such carbonate areas, phenomena and disciplines related to their study derives from the name of this region, which is called the Classical Karst (Gams 1993;

Cucchi 2004; Cucchi et al. 2015a). Yet, the absence of superficial waters is contrasted by the impressive presence of water in the underground, and water and carbonate substrates interact through a series of complex structures and dynamic processes. A peculiar karst phenomenon is represented by karst lakes, which are temporary lakes that seasonally disappear at certain times of the year and are characterized by strong oscillations of the water level, reaching up to several meters of variation. Temporary lakes of the Dinaric Karst are the expression on the sur-



face of the variations of the karst aquifer near areas of groundwater discharge (Pipan and Culver 2019).

Lake Doberdò is one of the few karst lakes in Italy, and one of the best-known at the international level. It is included among the regional sites of greatest geological interest and the geosites of supranational interest for geological-geomorphological conservation found in the Friuli Venezia Giulia region (Cucchi et al. 2009). It belongs to the karst lake system lying in the northwestern part of the Classical Karst, including also Lake Pietrarossa and two other wetlands, Lake Sablici and Lake Mucille, which were completely altered by the reclamation works carried out in the 1950s that heavily affected also Lake Pietrarossa. The lake is an example of Groundwater Dependent Ecosystems (GDE), crucial ecosystems for their high biodiversity and ecosystem services whose importance is recognized by EU legislation (Kløve et al. 2014), under the Water Framework Directive 2000/60/EC and the Groundwater Directive 2006/118/EC for the protection of Europe's water bodies, and the Habitats Directive 92/43/EEC and Birds Directive 2009/147/EC for biodiversity conservation. GDEs are valuable ecosystems for which current composition, structure and functions are dependent on a supply of groundwater (ARMCANZ and ANZECC 1996; Galassi and Stoch 2011).

The peculiar hydro-ecological nature of Lake Doberdò allows the presence of an impressive variety of species and habitats, also of high conservation value, thanks to its strong ecotonal character. The area is part of a Regional Nature Reserve and the Natura 2000 network. Lake Doberdò has been considered in many floristic and vegetation studies, however there is no work specifically

dedicated to this exceptional natural area. As for the aspects regarding the vegetation, a research coordinated by prof. L. Poldini was carried out in the late 1960s (Vascotto 1967), while the main aquatic and hygrophilous communities of the lake were discussed by Poldini (1989, 2009). A recent analysis of the occurrence of alien plant species in the different habitats of this wetland is available in Liccari et al. (2020).

This paper presents a comprehensive and updated analysis of the plant communities of Lake Doberdò based on a phytosociological survey. The aim of the work is to provide a robust knowledge base essential for the assessment of the conservation status of its habitats, their monitoring and the planning of conservation strategies to be undertaken also in response to the rising problem of climate change that is threatening wetlands at the global level.

## Materials and methods

### Study area

Lake Doberdò (Fig. 1, 45°49'51"N 13°33'44"E) is located in the NW part of the Classical Karst, in the municipality of Doberdò del Lago (NE Italy). The Classical Karst is a dry limestone plateau extending between Italy and Slovenia and is the northwesternmost part of the External Dinarides; the altitude degrades from average altitudes of 400-450 m a.s.l. in the SE sector to the sea level in the NW sector. It consists of a thick succession of carbonatic rocks (Lower Cretaceous to Lower Eocene), overlapped by a



**Figure 1.** Study area at low-water period (2011 orthophoto, from IRDAT FVG). The springs of the karst Lake Doberdò are concentrated in the West sector of the basin, with the two major spring pools visible to the NW (1-2); a stream flows through the polje, with a large pool (3) at the confluence of various spring-fed channels located in the central-eastern sector of the basin; the stream disappears in the swallow hole pools in the East sector (4: main swallow hole pool). The dashed yellow line corresponds to the seasonal highest water level.



clastic quartz-feldspar-limestone succession called Flysch (Eocene) (Samez et al. 2005, Zini et al. 2014; Cucchi et al. 2015b). It has a complex hydrostructure of hypogean waters; a spring system is located in the NW sector, where a karst lake system is found (Zini et al. 2015), including Lake Doberdò.

The Italian Karst has a moderate continental climate, showing mediterranean features along the coast. The annual average temperature (Sgonico weather station, 268 m a.s.l.) is ca. 12.5–13 °C; the monthly mean temperature ranges from ca. 3.5 °C (January) to ca. 23 °C (July–August); the absolute temperature values range from –8 °C to 35 °C. Annual precipitation ranges from 1200 mm in the coastal areas to 1400 mm in the inner part, with maximum monthly rainfall in the autumn (November) and the early summer (June), while the minimum rainfall occurs in February and July (Arpa FVG-OSMER 2015a, 2015b: 1961–2010 period). From a bioclimatic point of view, the Italian Karst lies in the Temperate Oceanic bioclimate, in weak semicontinental areas with upper mesotemperate thermotype and lower humid ombrotype (Pesaresi et al. 2017).

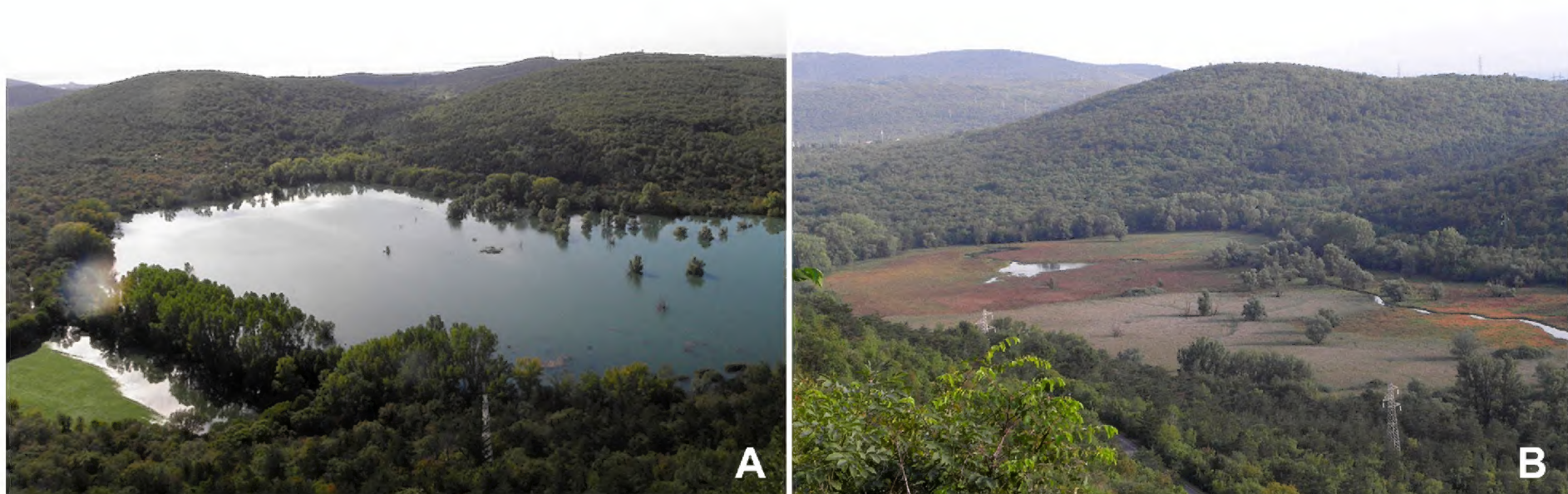
Lake Doberdò occupies the bottom of a NW-SE oriented polje (i.e. a large flat plain found in karst regions). The average water surface area (i.e. at normal water level) is ca. 35 ha and the average elevation of the lake is 4.5 m a.s.l. The geological substrate of the area belongs to the Monte Coste limestones (Cucchi et al. 2015b). The bottom of the lake is covered by a thick muddy layer produced by plant debris decomposed to different degrees; it is located above a layer of alluvial deposits consisting of silty-clayey sediments that can reach 4 to 5 m in thickness (Cucchi et al. 2009).

Lake Doberdò is a typical disappearing lake with no tributaries or outflowing rivers, being the result of the emersion of the groundwater. It has a typical strongly variable water regime (Fig. 2), with a water surface area that can vary even in few days between ca. 2 ha at low water level and 35 ha at normal water level, reaching up to ca. 47 ha at seasonal highest water level, and even more during exceptional floods; water level fluctuations can be higher than 6 m at seasonal high water periods. The water input

is mainly related to the fluctuations of the underground water recharged by precipitations prevailing during high water phases and by the input from the Isonzo alluvial aquifer prevailing during low water periods (Cucchi et al. 2000; Samez et al. 2005). Lake filling and flooding usually follow a seasonal trend related to the rainfall pattern, occurring in autumn–winter and early summer, while the lake usually empties in summer; however, the lake can flood at any time of the year, even in summer, in response of high rainfall events.

The water body has a very changeable dual nature, being a lake in some periods of the year and a shallow stream, formed by the confluence of various spring-fed channels, flowing through the polje during dry periods. Thus, the bottom of what is a lake at normal and high water periods turns to the floodplain of a small stream covered by typical marsh and grassland vegetation when the water level drops. After the lake empties, the floor vegetation appears, completely encrusted by silty-clay lacustrine sediments (Fig. 3). The lake fills and empties through springs and swallow holes (*ponors*). It is fed by perennial and intermittent springs found in the W sector; they are mainly small limnocrenes, but there are also perennial springs that open at the bottom of two large pools 6 m deep and ca. 150 and 260 m<sup>2</sup> wide (Fig. 1). Various swallow holes are found along the marginal parts of the lake, mainly in the E sector; some holes act both as springs and swallow holes in the different periods of the year (*estavelles*). During low water periods, the perennial stream disappears in the final SE swallow holes (Figs 1, 2B) which form some pools, the main one 4 m deep and ca. 11 m in diameter (Frenopoulos 1992).

In the past the lake appeared as a kind of wetland covered with a veil of water hidden by the luxuriant marsh vegetation for most part of the year (Fornasir 1929; Galli 2012), but at times of normal and high water fishes would appear, and fishing was an important economic activity for local people, who used to mow reed and sedge beds for different uses and to exploit the lake and its banks for grazing, getting hay or watering livestock (Scarpa and Blasich 2005; Visintin 2006). In the last decades the low water phases



**Figure 2.** A, Lake Doberdò at seasonal peak of high-water; B, Lake Doberdò at low-water period.





**Figure 3.** *Carex elata* tussocks and other vegetation types covered with lacustrine sediment near a swallow hole in the NE sector of the lake basin immediately after a period of flooding in winter.

last longer than in the past; among the possible causes of the change of the hydrological regime are the reclamation works carried out in the 1950s that affected the other wetlands of the lake system and river regulation works along the Isonzo River (Samez et al. 2005; Scarpa and Blasich 2005; Visintin 2006; Stoch 2011; Galli 2012). Due to several factors, the lake is slowly changing and drying.

The lake is surrounded by typical xerothermophilous Karst communities notably represented by the dry karst *Saturejion subspicatae* grasslands of *Centaureo cristatae*-*Chrysopogonetum grylli* and the *Aristolochio luteae*-*Quercetum pubescentis pistacietosum terebinthi* woodland. It is part of the Regional Nature Reserve of Doberdò and Pietrarossa Lakes and of the Natura 2000 sites SAC IT3340006 - Carso Triestino e Goriziano and SPA IT3341002 - Aree Carsiche della Venezia Giulia.

### Vegetation survey and data analysis

The vegetation survey was carried out according to the phytosociological approach (Braun-Blanquet 1964). A total of 177 relevés were carried out; field work was performed in April/October 2015-2018.

The study considered the plant communities related to the presence of the lake, from aquatic to meso-hygrophilous phytocoenoses, up to the parts of the banks subject to the peaks of seasonal high water, corresponding to a total area of ca. 47 ha. This area encompasses the permanently submerged zones and those periodically flooded on a seasonal basis including the whole littoral zone according to Hutchinson (1967) and Wetzel (2001). In a typical lake

zonation, meso-hygrophilous vegetation types usually correspond to the supralittoral zone; conversely, at Lake Doberdò these communities are flooded various times a year during the peaks of seasonal high water, and they can withstand the periodical inundations thanks to the short submersion periods and the underlying carbonate substrate which allows the soil to drain very fast after a flood: they are considered as the uppermost part of the eulittoral zone of the karst lake.

The present paper focuses on the herbaceous plant communities, including the aquatic, marsh and meso-hygrophilous vegetation types. In order to provide the full picture of lake-dependent coenoses, the woody communities are briefly summarized, the peculiar scrub and forest types observed at Lake Doberdò being discussed in Poldini et al. (2020).

The syntaxonomic attribution of the relevés was supported by statistical analyses using SYN-TAX 2000 (Podani 2001). The analysis of the matrices of relevés and species was performed on cover data, previously transformed according to Van der Maarel (1979). The set of relevés was subdivided into main groups of vegetation types on the basis of the different ecology and growth form: aquatic (67 relevés), hygrophilous and water edge pioneer annual (86), meso-hygrophilous perennial (18) and bryophyte (6) communities. The phytosociological analysis of the first two, larger groups of relevés, characterized by high diversity of stands, was supported by the analysis of the two data matrices by means of agglomerative hierarchical clustering using Chord distance as resemblance measure and group average linkage method (UPGMA). The interpretation of a peculiar hay meadow was based on the



comparison with published and unpublished relevés of similar coenoses from NE Italy by means of agglomerative hierarchical clustering as above and Principal Component Analysis (PCA, correlation method).

Syntaxonomic nomenclature up to the level of alliance follows Biondi and Blasi (2015) and updates (Poldini et al. 2020); nomenclature and organization of associations follow mostly Chytrý (2011), Info Flora (2020), and in particular Chytrý (2011) for *Lemnetea*, Sburlino et al. (2008), Šumberová (2011a) and Felzines (2016) for *Potamoetea*. Classification and nomenclature of associations of the class *Phragmito-Magnocaricetea* follow Landucci et al. (2020). For bryophyte communities the syntaxonomic scheme up to alliances is in accordance with Mucina et al. (2016), while the nomenclature of the associations follows Puglisi and Privitera (2012).

Nomenclature of species follows Bartolucci et al. (2018) and Galasso et al. (2018) for vascular plants, Aleffi et al. (2020) for mosses. Subspecies are reported in the text only when they are different from the nominal subspecies or when one or more subspecies occur beside the nominal one.

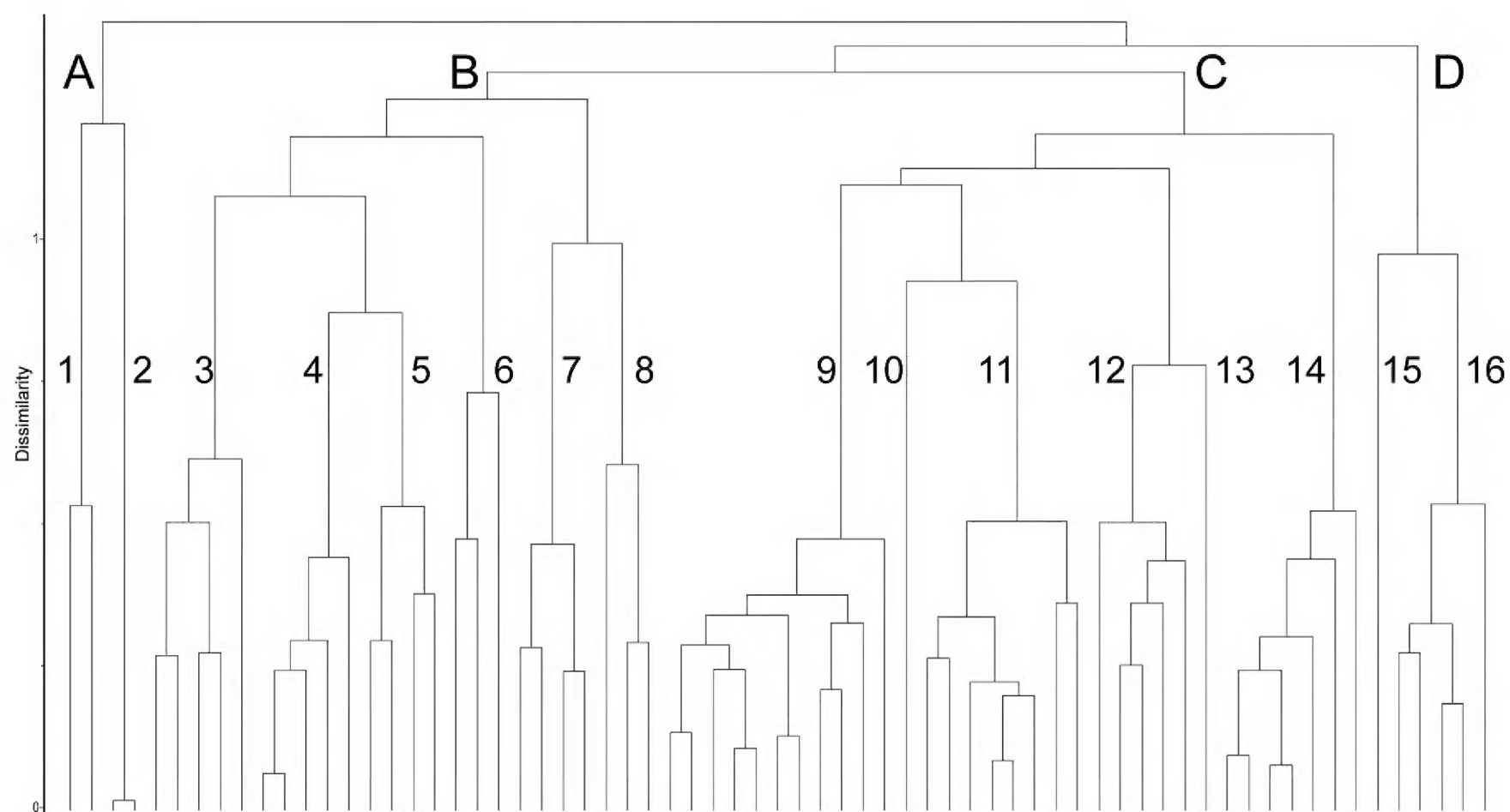
The correspondence of plant communities with habitats of the 92/43/EEC Habitats Directive follows the European Interpretation Manual (European Commission 2013), EUNIS (2020) and Biondi et al. (2009, 2012).

## Results and discussion

### Cluster analysis

The cluster analysis of the relevés of aquatic vegetation allowed to recognize 16 groups of stands which were attributed to distinct communities (Fig. 4). They are arranged in four main clusters, characterized as follows. Cluster A includes the stands dominated by the pleustophytes *Lemna minor* or *Ceratophyllum demersum*; cluster B includes the stands of different vegetation types correlated to spring water, found in the spring pools, their brooks and the upper course of the main stream in clear, oxygenated, oligo-mesotrophic, slowly to moderately flowing waters, mainly corresponding to *Batrachion fluitantis* communities; cluster C gathers stands dominated by various species found in the middle and lower course of the main stream as well as the final swallow hole pools, in more eutrophic, often turbid, slow flowing to standing water, corresponding to the ecological features of *Potamion* and *Ranunculion aquatilis* communities; cluster D includes stands of *Nuphar lutea* or *Potamogeton pusillus* found in standing, eutrophic, often turbid water of pools located in the eastern part of the basin where the swallow holes lie.

The cluster analyses of marsh and water edge annual pioneer vegetation allowed to point out 16 groups of stands (Fig. 5), which can be attributed to 12 emergent



**Figure 4.** Cluster analysis of relevés of aquatic vegetation (cover data, Chord distance, UPGMA): 1, *Lemnetum minoris*; 2, *Ceratophylletum demersi*; 3, *Lemnetum trisulcae*; 4, *Potamo perfoliati-Ranunculetum fluitantis*; 5, *Ranunculo trichophylli-Callitrichetum polymorphae*; 6, *Parvopotamo-Zannichellietum palustris*; 7, *Hippuris vulgaris* f. *fluviatilis* community; 8, *Veronico beccabungae-Callitrichetum stagnalis*; 9, *Potametum lucentis*; 10, *Potamo crisp-Myriophylletum verticillati*; 11, *Ranunculo circinati-Elodeetum nuttallii*; 12, *Potametum pectinati*; 13, *Potamo crisp-Ranunculetum trichophylli*; 14, *Ranunculo circinati-Myriophylletum spicati*; 15, *Potametum pusilli*; 16, *Nymphaetum albo-luteae*.



communities of the class *Phragmito-Magnocaricetea* and 2 pioneer associations of the classes *Bidentetea* and *Isoëto-Nanojuncetea*, some coenoses occurring with different aspects.

## Plant communities of Lake Doberdò

### PERMANENTLY TO INTERMITTENTLY SUBMERGED BRYOPHYTE VEGETATION (CLASS PLATYHYPNIDIO-FONTINALIETEA ANTIPYRETICAE)

**FONTINALETUM ANTIPYRETICAE** Kaiser ex Frahm 1971 (Suppl. material 1, Table S1, rels 1–4)

This aquatic community typically grows in slow-flowing or still waters on submerged rocks, stones, or parts of trees, or on the bottom of shallow waters. *Fontinalis antipyretica* occurs in a wide range of water bodies, light availability and water quality, and tolerates periods of emersion (Atherton et al. 2010).

At Lake Doberdò this species-poor or monospecific community is made up of more or less loose masses of *F. antipyretica*. It occurs in mesotrophic to eutrophic waters in the central and eastern part of the lake basin: it is found growing submerged in the moderately to slowly flowing waters of the main stream and it also covers the calcareous rocks which form the bottom and the banks of the final swallow hole pools, where it is periodically submerged by almost still, turbid waters and exposed at dry periods. Moreover it is rather common at the base of the tussocks of *Carex elata* in the E part of the basin, which is the area

most subject to water level fluctuation. It is in catenal contact with aquatic communities of *Lemnetea* (*Lemnetum minoris*) and *Potametea*, and helophytic communities (*Caricetum elatae*, *Schoenoplectetum lacustris*).

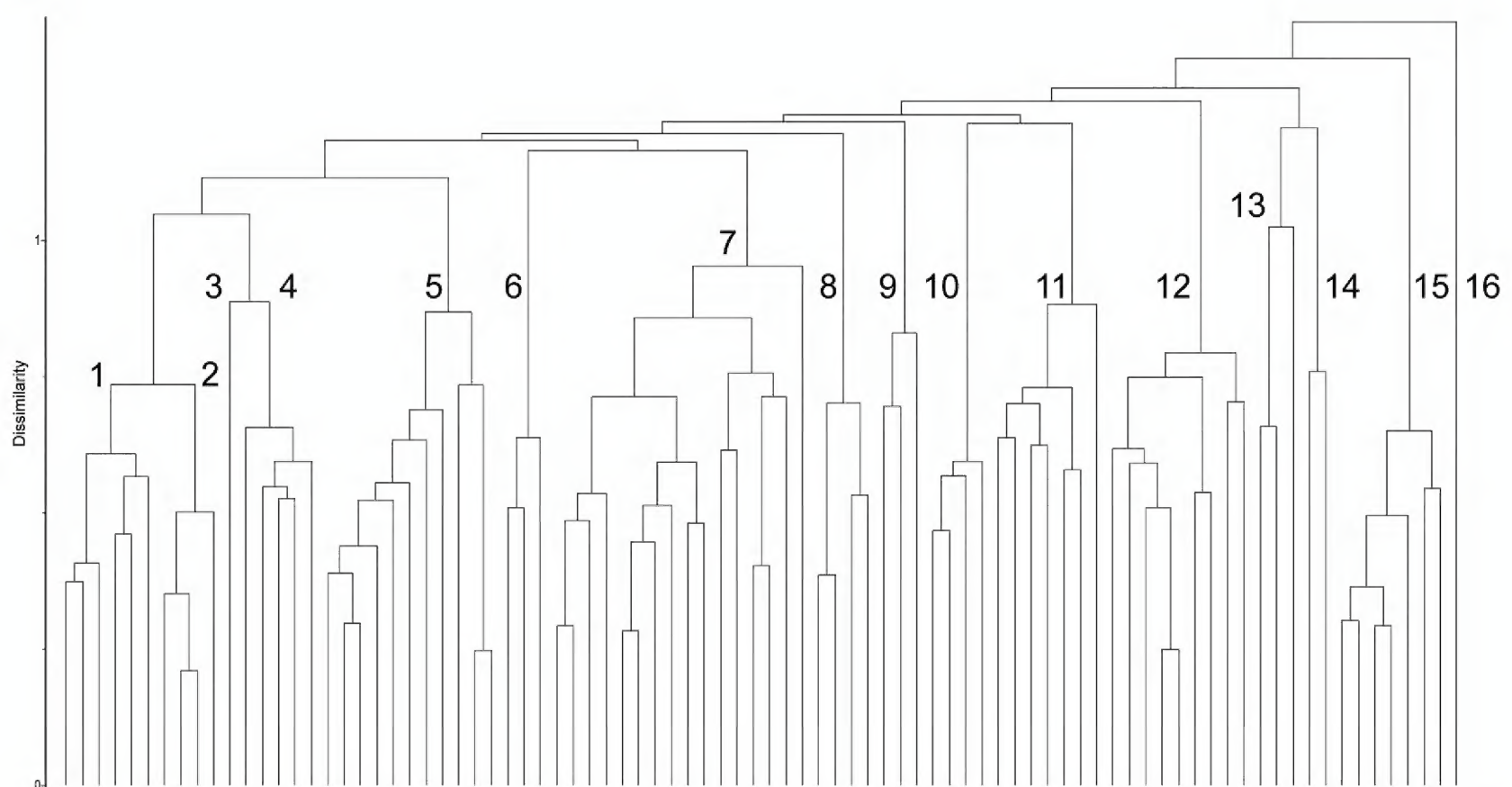
**Annex I Habitat (92/43/EEC Directive):** The community of Lake Doberdò can be referred to habitats 3150, 3260.

**CINCLIDOTETUM FONTINALOIDIS** Gams ex v. Hüb-schmann 1953 (Suppl. material 1, Table S1, rels 5–6)

This association grows on river and lake shores on intermittently but frequently submerged rocks, tree roots, stonework; it is found under various light conditions and can tolerate prolonged periods of exposure (Schubert 2009; Atherton et al. 2010).

At Lake Doberdò this species-poor community occurs as large monospecific stands of *Cinclidotus fontinaloides*. It represents the typical amphibious bryophyte vegetation of the limnocrenes: it covers the rocks of the bottom of the springs and their brooks, but it also thrives on roots, trunks and low branches of trees up to a few meters high from the ground that are regularly flooded by the rising of the water. It is common in the W part of the basin, where the karst springs lye, growing in clear, oligo-mesotrophic waters. It is in contact with *Lemnetea* (*Lemnetum trisulcae*) and *Phragmito-Magnocaricetea* (*Caricetum elatae*, *Beruletum erectae*) communities.

**Annex I Habitat (92/43/EEC Directive):** *Cinclidotus fontinaloides* along with *Fontinalis antipyretica* are the two plant species listed as characteristic of the habitat type 3180\*-Turloughs (European Commission 2013) (see discussion on conservation aspects).



**Figure 5.** Cluster analysis of relevés of marsh and water edge pioneer annual vegetation (cover data, Chord distance, UPGMA): 1, *Polygonetum hydropiperis*, *Persicaria hydropiper*-dominated stands; 2, *Leersietum oryzoidis*, wetter stands with *Persicaria hydropiper*; 3, *Typhetum latifoliae*; 4, *Leersietum oryzoidis*, drier stands from lake margins; 5, *Persicaria amphibia* f. *terrestre* community; 6, *Iridetum pseudacori*; 7, *Caricetum elatae*; 8, *Glycerio-Sparganietum neglecti*; 9, *Eleocharitetum palustris*; 10, *Phalaridetum arundinaceae*; 11, *Caricetum vesicariae*; 12, *Schoenoplectetum lacustris*; 13, *Polygonetum hydropiperis*, *Bidens frondosa*-dominated stands from lake margins; 14, *Cyperus fuscus* community; 15, *Phragmitetum australis*; 16, *Beruletum erectae*.



## AQUATIC VEGETATION OF FREE-FLOATING PLANTS (CLASS LEMNETEA MINORIS)

*LEMNETUM MINORIS* Soó 1927 (Suppl. material 1, Table S2, rels 1–2)

In the study area the coenosis is rare and occurs in shallow waters with lentic character in the central and eastern sectors, mainly in the final swallow hole pools; its presence is strongly variable throughout the years, depending on the water regime trend. It is in catenal contact with submerged and floating-leaved *Potametea* communities, *Fontinaletum antipyreticae* and helophytic communities (*Schoenoplectetum lacustris*).

*Annex I Habitat (92/43/EEC Directive):* 3150.

*LEMNETUM TRISULCAE* Den Hartog 1963 (Suppl. material 1, Table S2, rels 3–7)

At Lake Doberdò *L. trisulca* forms dense mats floating just below the water surface, often mixed with *Callitriche cophocarpa*. The community occurs in the small limnocrenes and in the upper and middle parts of the brooks flowing from them, in the W part of the basin; at low-water periods the water level is ca. 40–70 cm but in some stretches it can drop to 10 cm. It is found in clear, oligo-mesotrophic, standing or slow-flowing spring waters, generally in shaded sites within the lakeshore woods with *Salix alba* or with *Ulmus minor*; it is also found in the N sector in a small, rather deep sunlit pool with clear water, where it is shaded by the floating leaves of *Nuphar lutea*. It is in contact with various aquatic *Potametea* communities, *Cinclidotetum fontinaloides* and *Phragmito-Magnocaricetea* beds bordering the spring pools and their brooks.

*Annex I Habitat (92/43/EEC Directive):* 3150, 3260.

## AQUATIC VEGETATION OF ROOTED PLANTS (CLASS POTAMETEA PECTINATI)

*Batrachion fluitantis* communities typical of running waters occur in the W sector, where the karst springs and their brooks lay, while communities typical of slow-running or standing waters of *Potamion pectinati*, *Nymphaeion albae* and *Ranunculion aquatilis* dominate the central-eastern sector. *Potamion* communities growing in the moderately to slowly running waters of the spring brooks and the main stream were attributed to Annex I habitat 3260 in accordance with Poldini et al. (2006), Felzines (2016) and EUNIS (2020).

*POTAMETUM LUCENTIS* Hueck 1931 (Suppl. material 1, Table S3, rels 1–11)

In the study area this submerged community is dominated by *Potamogeton lucens* often accompanied by *Elodea nuttallii*, *Stuckenia pectinata* and *Myriophyllum spicatum*. It is widespread in the moderately to slowly running, meso-eutrophic waters along the whole main stream, occurring also in some stretches of the larger spring brooks. It is found mainly on silt-clay beds; water level at dry periods is ca. 60–80 cm. It thrives in open sites, but it is able to

tolerate moderate shade conditions within the lakeshore woods. It is found in catenal contact with submerged communities of *Potamion pectinati* (esp. *Potametum pectinati*), *Batrachion fluitantis* and helophytic vegetation (*Phragmito-Magnocaricetea*).

*Annex I Habitat (92/43/EEC Directive):* 3260.

*POTAMETUM PECTINATI* Carstensen ex Hilbig 1971 (Suppl. material 1, Table S3, rels 12–16)

*Stuckenia pectinata* is found in a wide range of habitats and is extremely variable in growth form: several forms of this entity have been described, however much of the variation is due to phenotypic plasticity or ontogenic variation and most of the characters used in the classifications of its wide morphological variation proved to be dependent simply on environmental conditions (Preston 1995; Kaplan 2002, 2008). Most records of *S. pectinata* communities from Italy are attributed to *Potametum pectinati*, a species-poor association of the *Potamion* alliance reported from mesotrophic to hypertrophic, standing to slow-flowing waters and characterized by the typical growth form of the species. However, in NE Italy another coenosis has been pointed out and attributed to *Sparganio emersi-Potametum pectinati* (syn.: *Sparganio-Potametum interrupti*), belonging to *Batrachion fluitantis* (Sburlino et al. 2008): it occurs in slow to definitely running waters and is characterized by *S. pectinata* f. *interrupta*, a rheophile form with elongated stems and larger leaves (see e.g., Schubert et al. 2001; Sburlino et al. 2008). According to Kaplan (2008) this form has no taxonomic value; nevertheless, the rheophile phenotypes of *S. pectinata*, along with those of other species, characterize *Sparganio-Potametum pectinati* (Felzines 2016).

The classification of the *S. pectinata* community found in the study area was not easy: its physiognomy and floristic composition resemble some relevés of *Sparganio-Potametum interrupti* published by Sburlino et al. (2008); in the stream phase (i.e. at low-water periods) it is found in moderately flowing waters; the individuals show a habitus similar to that of running waters but the leaves are narrower than 1 mm, corresponding to those of the typical growth form related to standing waters. These intermediate morphological features could be due to the strongly variable nature of the water body. Moreover the stands are poor in species, which does not support a univocal interpretation. The community was attributed to *Potametum pectinati* taking account of the moderate to very slow water flow of the stands, the low presence of *Batrachion fluitantis* elements, the occurrence of *Potamion coenoses* in this part of the basin and the peculiarity of the karst water body.

At Doberdò the community, dominated by *S. pectinata* often accompanied by *Elodea nuttallii*, appears in the middle course of the main stream, but becomes more frequent in the lower course and in the final pools, where the nutrient load increases. It is found in the central parts of the channel, in moderately flowing to almost standing eutrophic waters, on silty-clayey bottom. It grows in moderately clear and deep waters (70–80 cm deep at low-water),



but it is able to flourish also in the shallow, turbid water of the margins of the final swallow hole pool. It is found in the central and eastern parts of the basin, where it seems to have largely replaced the *Myriophyllum spicatum*-dominated stands widespread in the past (see comment to *Ranunculo circinati-Myriophylletum spicati*), in analogy to what observed for Central Italy (see Landucci et al. 2011). It is in contact with *Potametum lucentis* and *Ranunculo-Myriophylletum spicati* in the main stream, and with *Nymphaeetum albo-luteae* and *Potamo crisp-Ranunculetum trichophylli* in the final pools, respectively toward deeper and shallower water.

*Annex I Habitat (92/43/EEC Directive):* 3150, 3260.

**POTAMETUM PUSILLI** Soó 1927 (Suppl. material 1, Table S3, rel. 17)

*Potametum pusilli* includes species-poor *Potamogeton pusillus*-stands occurring in standing to slow running, neutral to basic, mesotrophic to eutrophic, and even oligo-saline waters, on sandy to clayey substrates covered by a more or less calcareous mud (Šumberová 2011a; Felzines 2016).

The circumscription of the association follows Felzines (2016). The community consists of almost monospecific large stands of *P. pusillus* accompanied by a few other species with low cover. It is rare, being found only in the main, largest pool in the central-eastern sector of the basin, where it grows in the sunlit peripheral, shallow and almost standing, eutrophic, very turbid waters on muddy bottom. It is in contact with *Ranunculo-Myriophylletum spicati*, waterward also with *Nymphaeetum albo-luteae* and *Ranunculo-Elodeetum nuttallii*.

*Annex I Habitat (92/43/EEC Directive):* 3150.

**PARVOPOTAMO-ZANNICHELLIETUM PALUSTRIS** Koch ex Kapp & Sell 1965 **GROENLANDIETOSUM DENSAE** (Cirujano, Pascual & Velayos 1986) Felzines 2016 (Suppl. material 1, Table S3, rels 18–20)

The syntaxonomy of *Zannichellia palustris* s.l. communities is problematic both for ecological and taxonomic reasons related to the critical treatment of the genus (Sburlino et al. 2008). Bartolucci et al. (2018) separate *Zannichellia pedunculata* Rchb., corresponding to the subsp. *pedicellata* and related to *Zannichellion pedicellatae* communities of brackish coastal habitats, and *Zannichellia palustris* L., which includes the nominal and the *polycarpa* subspecies. Communities from Italy not characterized by *Z. pedunculata* have been generally attributed to *Zannichellietum palustris*, related to still or slow-running, strongly eutrophic waters on clayey bottoms. Sburlino et al. (2008) highlighted in NE Italy *Z. palustris* subsp. *palustris* stands with a peculiar ecology linked to shallow spring watercourses of the high and low plain, assigned to *Batrachion fluitantis* and attributed to *Ranunculo-Zannichellietum palustris*, an association described from clear, basic, slow-flowing to flowing waters of small streams and ditches of Germany on sandy-gravelly beds. However, Felzines (2016) treats both *Zannichellietum palustris* and

*Ranunculo-Zannichellietum* as synonyms of *Parvopotamo-Zannichellietum palustris*, which he regards as a rather variable *Potamion* coenosis with some aspects still in need of in-depth syntaxonomic analysis, found in standing to weakly flowing, shallow to medium-deep, meso- to eutrophic or even hypertrophic, neutral to basic water, on sandy to loamy substrate, tolerant to pollution and water level fluctuations. The original relevés of *Ranunculo-Zannichellietum* by Passarge (1996) are included by Felzines (2016) in the subass. *groenlandietosum densae*.

The community from Lake Doberdò agrees both floristically and ecologically with the stands reported by Sburlino et al. (2008), although the plants correspond to the subsp. *polycarpa* (with no taxonomic value according to the recent treatments) and the coenosis is found on fine bottom sediments. Pending a syntaxonomic clarification, it is attributed to *Parvopotamo-Zannichellietum palustris groenlandietosum densae*, although we think that it could be better included in *Batrachion fluitantis*, as done by Sburlino et al. (2008), also considering the contact with communities of this alliance. It includes submerged species-poor stands made up of large and dense masses of *Zannichellia palustris* often mixed with abundant *Callitriche cophocarpa*, along with *Ranunculus trichophyllus* and scattered clumps of *Lemna trisulca*. It thrives in the main spring brooks and in few spots in the upper and middle course of the main stream, in moderately flowing, mesotrophic, rather clear, relatively shallow waters (ca. 60 cm deep in dry periods) on silty-clayey bottoms. It is in contact with communities of medium- to slow-running waters (*Batrachion fluitantis*, *Potamion pectinati*), notably *Potamo-Ranunculetum fluitantis*, and *Phragmito-Magno-caricetea* vegetation.

*Annex I Habitat (92/43/EEC Directive):* 3260.

**RANUNCULO CIRCINATI-MYRIOPHYLLETUM SPICATI** Tomasz. ex Passarge 1982 (Suppl. material 1, Table S3, rels 21–27)

The treatment of *Myriophyllum spicatum*-communities is controversial: in this study we followed Felzines (2016). *Ranunculo-Myriophylletum* usually grows in mesotrophic to eutrophic, lime-rich, shallow to moderately deep standing waters, in open sites affected by regular mechanical disturbances or representing early succession phases, and it is able to tolerate turbidity, strong water level fluctuation and periodic emergence (e.g. Šumberová 2011a; Lastrucci et al. 2012; Felzines 2016; Info Flora 2020).

At Doberdò *M. spicatum* forms submerged species-poor stands, where it can be present with scattered to dense cover; it is often accompanied by *Elodea nuttallii*, *Stuckenia pectinata*, *Potamogeton lucens*, *Myriophyllum verticillatum*, *Ranunculus trichophyllus*. The community is found in slow-flowing to almost standing, rather clear to turbid, shallow to moderately deep waters (up to 80 cm deep in dry periods), on muddy silt-clay beds, in fully lit, meso-eutrophic to eutrophic situations. It grows in almost standing water along the margins of the main stream and of the large final pools as sparse, almost monospecific



stands, but it is also found with high cover values in the central parts of the channel in the middle and lower reaches of the main stream, where the water flow slows down significantly, in mosaics with other *Potamion* communities. The community is able to tolerate the periodical drying. It is particularly spread in the E sector, characterized by slower, more eutrophic and turbid waters. In the past, in this part of the main stream similar *M. spicatum*-dominated stands were widespread: they were interpreted as a variant of *Nymphaeetum albo-luteae* rich in *Myriophyllum spicatum* with little *Nuphar lutea* and *Nymphaea alba* linked to stretches with higher water speed compared to the typical lentic conditions of this association (Vascotto 1967; Poldini 1989). At present no plants of floating-leaved species are observed, which suggests a change in the water regime, resulting also in the evident contraction of *Nymphaeetum* (see comment to this community). *Ranunculo-Myriophylletum* is therefore here a stable vegetation type, which however has become poorer in species with the disappearance of *Nuphar lutea*, *Nymphaea alba* and *Hottonia palustris*. It is in catenal contact in slow-flowing waters with other *Potamion* communities, in the standing waters of the swallow hole pools with *Nymphaeetum albo-luteae* waterward, and with *Potamo crispus-Ranunculetum trichophylli* towards the margins; it is in contact also with helophytic communities (*Schoenoplectetum lacustris*, *Persicaria amphibia* f. *terrestre* community).

*Annex I Habitat (92/43/EEC Directive):* 3150, 3260.

**POTAMO CRISPI-MYRIOPHYLLETUM VERTICILLATI**  
Soó 1928 (Suppl. material 1, Table S3, rel. 28)

*Myriophyllum verticillatum* vegetation observed in the study area agrees with *Potamo-Myriophylletum verticillati* (see Felzines (2016); Info Flora (2020)), a vegetation reported from standing to slow-flowing, mesotrophic to naturally eutrophic, shallow to moderately deep, clear waters in alluvial pools, ponds, channels, lentic parts of streams, on silty-clayey bottom. It is linked to lentic habitats being filled up, replacing *Myriophyllum spicatum* which occurs in earlier or pioneer stages of the succession (Šumberová 2011a; Info Flora 2020).

In the survey area the community is made up by *M. verticillatum*, which shows an extensive growth filling the whole water column with dense masses, mixed with rather abundant *Elodea nuttallii*. It was observed in a single site, in a small lateral branch of the middle course of the stream heading to a temporary swallow hole, in almost stagnant, eutrophic, rather turbid, moderately deep water (ca. 70 cm at dry periods), on silty-clayey muddy bottom, in contact with *Ranunculo-Elodeetum nuttallii* and *Caricetum elatae* bordering the water stretch.

*Annex I Habitat (92/43/EEC Directive):* 3150.

**RANUNCULO CIRCINATI-ELODEETUM NUTTALLII**  
De Lange in Passarge 1994 (Suppl. material 1, Table S3, rels 29–36)

*Ranunculo-Elodeetum nuttallii* is a submerged community often consisting of very dense masses of *E. nuttallii*.

It is a heliophilous coenosis, resistant to eutrophication and pollution, found in standing to slow-flowing, shallow waters (0.20–1.20 m deep); it grows in meso-eutrophic to eutrophic, turbid, strongly mineralized, neutral to basic waters rich in calcium and it is a pioneer community in water bodies mechanically disturbed (Felzines 2016; Info Flora 2020). The association was first described by De Lange (1972) from ditches of the Netherlands, with *E. nuttallii* and *Ranunculus circinatus* as the characteristic species, and was subsequently validly published in Passarge (1994). Later, Ciocârlan et al. (1997) described from Romania a substantially corresponding community, *Ceratophyllo demersi-Elodeetum nuttallii*, found in lakes, channels and ditches in standing waters with a high level of eutrophication, in which *E. nuttallii* can form monospecific stands or can be mixed with few submerged species, more frequently *Ceratophyllum demersum*, *Stuckenia pectinata* and free-floating species such as *Lemna minor* and *Spirodela polyrrhiza*.

*E. nuttallii* is native to North America and was unintentionally introduced in Europe as an aquarium plant: first reported in Belgium in 1939, it is rapidly spreading throughout the continent displacing the close alien species *E. canadensis* in many localities (CABI 2020). It is able to form extensive monospecific and dense mats, excluding other native species, invading aquatic habitats and rapidly producing a huge amount of biomass that can seriously alter environmental conditions. It is included in the list of the Invasive Alien Species of Union concern in accordance with the EU Regulation 1143/2014. As for Italy, *E. nuttallii* was first recorded in 1989 from Lake Idro, Lombardy (Desfayes 1995) and at present it is considered an invasive species (Galasso et al. 2018). It was recorded in Friuli Venezia Giulia in 2011 from Lake Doberdò (Martini 2014), where it seems to have completely displaced *E. canadensis*.

At Lake Doberdò *E. nuttallii* forms thick and large monospecific mats, tending to occupy the whole available area and to replace the other submerged species. The community shows a broad ecological amplitude being spread in a wide range of habitats, in still to moderate-flowing waters throughout the whole basin, from the springs and their brooks to the main stream and the final swallow hole pools. It thrives on muddy bottoms in sunlit waters but it is found in shaded sites as well. It is able to tolerate strongly turbid water, confirming a shade-tolerant character: *E. nuttallii* is one of the few species found in the deeper parts of the large pool which stands out in the central-eastern part of the basin, characterized by eutrophic, strongly turbid waters. The species seems to be able to tolerate prolonged emersion during the dry periods. The community is in contact with many aquatic communities such as *Lemnetum minoris*, *Potametum lucentis*, *Ranunculo-Myriophylletum spicati*, *Potamo-Myriophylletum verticillati*, *Potamo-Ranunculetum fluitantis*, and with *Phragmito-Magnocaricetea* vegetation (esp. *Schoenoplectetum lacustris*, *Caricetum elatae*). Up to our knowledge this is the first record of the association in Italy.



*Annex I Habitat (92/43/EEC Directive):* -. The community occurs as a threat in habitats 3150 and 3260.

*NYMPHAEETUM ALBO-LUTEAE* Nowiński 1928 (Suppl. material 1, Table S4, rels 1–5)

This rather variable association includes stands dominated or codominated by *Nuphar lutea* and/or *Nymphaea alba*, found in standing to slow-flowing, mesotrophic to eutrophic, neutral to basic waters, on silty bottom rich in organic matter (Sburlino et al. 2008; Felzines 2016).

The observed, species-poor stands correspond to the typical aspects of the association dominated by *Nuphar lutea*, while *N. alba* appears sporadically. The community grows in standing or almost standing waters in the main pools lying along the stream in the E sector of the basin, where the movement of the water tends to transport sediments and nutrients, resulting in more eutrophic conditions. Indeed, the *Nuphar lutea* facies of the association is connected with higher water eutrophication than the facies dominated by *Nymphaea alba* (Sburlino et al. 2008), a species which however was once much more frequent in the study area (Vascotto 1967; Poldini 1989). The coenosis occurs also in some small pools in the N sector, surrounded by *Phragmites* beds. It is in contact towards the centre of the main pools with *Ceratophylletum demersi* and towards the outer zones with *Potametum pusilli*, *Potametum pectinati*, *Ranunculo-Myriophylletum spicati* and with *Potamo-Ranunculetum trichophylli*; towards the water edges it is also in contact with helophytic communities (*Phragmites* or *Schoenoplectus* beds, *Caricetum elatae*, *Persicaria amphibia* f. *terrestre* belt).

*Annex I Habitat (92/43/EEC Directive):* 3150.

*POTAMO CRISPI-RANUNCULETUM TRICHOPHYLLI* Imchenetzky 1926 (Suppl. material 1, Table S4, rel. 6)

This association prefers standing or slow-flowing, shallow waters and shows a wide ecological range in relation to water chemistry and dynamics, water level fluctuations and substrate, being able to tolerate periodic flooding and drying, and high water turbidity (Šumberová 2011a; Felzines 2016). The classification of the association within *Ranunculion aquatilis* follows Šumberová (2011a).

A species-poor but rather dense *Ranunculus trichophyllus*-dominated stand observed in the shallow waters of the main swallow hole pool was attributed to this association: the dominant species is mixed mainly with few elodeids. The community colonizes the muddy exposed banks and the shallow, warm, slightly flowing to standing waters of the margins of the swallow hole pool from which the last part of the stream heads to the final swallow hole, in the E part of the basin. It grows in the most eutrophic and turbid water of the study area and it is subject to frequent and wide fluctuations of water levels, long periods of drying and trampling by animals. Its development is considerably variable over the years depending on the water regime. It is in contact with *Nymphaeetum albo-luteae* toward the inner parts of the pool, *Ranunculo-Myriophylletum spicati* and *Potametum pectinati* in the shallow

marginal waters, and the emergent *Persicaria amphibia* community landward.

*Annex I Habitat (92/43/EEC Directive):* 3260.

*POTAMO PERFOLIATI-RANUNCULETUM FLUITANTIS* Allorge ex Koch 1926 *GROENLANDIETOSUM DENSISAE* (Imchenetzky 1926) Felzines 2016 (Suppl. material 1, Table S5, rels 1–5)

Stands dominated by *Ranunculus trichophyllus* found in the spring brooks of Lake Doberdò correspond well with the coenosis reported as *Ranunculo-Sietum erecto-submersi* by Poldini (1989) and *Ranunculo trichophylli-Sietum submersi* by Sburlino et al. (2008) from clear, calcareous, meso-eutrophic waters of watercourses, notably with the facies of the association without *Berula erecta*. However, they are reported following Felzines (2016), who includes *Ranunculo-Sietum* in *Potamo perfoliati-Ranunculetum fluitantis*, a rather variable association of more or less fast-flowing water highly characterized or dominated by *Batrachion* species, while *Berula erecta* may be frequent or absent. The stands from Lake Doberdò seem to be an impoverished, species-poor form of small spring watercourses subject to strong water level fluctuations and they are likely to represent a degraded aspect of a previous, more typical vegetation, considering that in the past in the same stretches *Potamogeton nodosus* was common (Vascotto 1967; Poldini 1989). *R. trichophyllus* forms large and dense mats filling the entire water column up to the water surface, and is accompanied by often abundant *Callitriche cophocarpa*, *Elodea nuttallii*, *Lemna trisulca*. The community is found in the central part of the larger brooks close to the springs (W sector), in slow- to medium-flowing, rather clear, mesotrophic calcareous waters, 50–70 cm deep at dry periods, on silty beds with scattered stones, generally in open but also in slightly shaded sites within the lakeshore *Salix alba* and *Ulmus minor* woods. It is in contact with *Potamion pectinati* and *Batrachion fluitantis* communities, notably *Parvopotamo-Zannichellietum* and *Ranunculo trichophylli-Callitrichetum polymorphae*, and with helophytic communities, in particular with *Glycerio-Sparganietum neglecti*.

*Annex I Habitat (92/43/EEC Directive):* 3260.

*HIPPURIS VULGARIS* F. *FLUVIATILIS* community (Suppl. material 1, Table S5, rels 6–9)

*Hippuris vulgaris* is well-adapted to water fluctuations and occurs in a wide range of conditions, being best related to clear, cool, oxygenated, neutral to alkaline, calcareous meso-eutrophic waters: it occurs on exposed banks, in marshes, flooded areas or shallow to deep water of lakes, ponds, ditches or streams (e.g. Preston and Croft 1997; Šumberová and Hroudová 2011). It is reported from standing waters (e.g. Rübel 1912; Görs 1992; Julve and Catteau 2007) but also from spring ponds fed by groundwater, flowing waters of small spring streams (mainly limnocrenes) or along tributaries of the Danube in the Alpine foothills (Pott 1995; Westermann and Westermann 1998), showing a relationship with habitats with water move-



ments, both as vertical fluctuations or as moderate, laminar flows. The classification of the coenoses dominated by *H. vulgaris* is therefore tricky and still controversial. Some authors regard both submerged and emergent or exposed stands as a single association, *Eleocharito palustris-Hippuridetum vulgaris*, assigned to *Phragmito-Magnocaricetea* (Šumberová and Hroudová 2011); other authors distinguish the emergent stands from the aquatic ones, which are usually reported as linked to lentic habitats and attributed to *Nymphaeion albae*, *Ranunculion aquatilis* or, recently, *Potamion pectinati* (see Sburlino et al. 2008; Felzines 2016). Yet, Sburlino et al. (2008) reported from NE Italy, including Lake Doberdò, a vegetation type from flowing spring waters, and attributed it to *Batrachion fluitantis* as a *H. vulgaris* phytocoenon. Felzines (2016) assigns all the aquatic *H. vulgaris*-dominated communities, including the *H. vulgaris* f. *fluviatilis* community pointed out by Sburlino et al. (2008), to *Myriophyllo verticillati-Hippuridetum vulgaris*, which he enlarges with respect to the original meaning by Julve and Catteau (2007) and moves from *Nymphaeion albae* to *Potamion pectinati*. On one hand, this solution could allow to include in a single association all the variability of the aquatic stands, related to the ecological plasticity of the dominant species and the highly changeable environmental conditions of its typical habitats; on the other hand, it could represent an oversimplification not reflecting the difference in the ecology of the coenoses. Consequently, we prefer to maintain the autonomy of the *H. vulgaris* community of Sburlino et al. (2008) and to refer the stands of Lake Doberdò to this spring-water *Batrachion fluitantis* vegetation also on account of the observed contacts, although recognizing that they exhibit features intermediate between *Batrachion* and *Potamion* communities, difficult to handle.

The stands of Lake Doberdò are species-poor and *H. vulgaris* is generally accompanied by *Callitriche cophocarpa*, *C. stagnalis*, *Elodea nuttallii*. The species can be present in low-water periods with completely submerged and curved stems or with erect stems with only the uppermost part emerging from the water. Most stands correspond to a facies of the community without *Berula erecta*, which however is present in a stand along a small spring brook. The coenosis forms linear belts along the water margins, in open to slightly shaded sites, in moderate- to slow-flowing waters near the springs: it occurs in the lower stretches of the brooks flowing from small limnocrenes, along the margins of the two major spring pools and in the upper part of the main stream immediately close to them. It grows in (oligo-)mesotrophic, clear, deep to fairly shallow waters, on silty muddy beds partly with stones, showing a clear relationship with conditions characterized by a moderate flow of cool, oxygenated spring water. It is in contact with submerged communities of moderately flowing waters of *Batrachion fluitantis* (esp. *Veronico beccabungae-Callitrichetum stagnalis*) and *Potamion pectinati* and helophytic vegetation (*Schoenoplectetum lacustris*, *Phragmitetum australis*, *Eleocharitetum palustris* and *Caricetum elatae*).

*Annex I Habitat (92/43/EEC Directive): 3260.*

**VERONICO BECCABUNGAE-CALLITRICHETUM STAGNALIS** Oberdorfer ex Müller 1962 (Suppl. material 1, Table S5, rels 10–12)

*C. stagnalis*-dominated communities are reported in Italy from clear, slightly flowing, often cool spring waters but also from lentic habitats (e.g. Corbetta and Pirone 1989; Baldoni and Biondi 1993; Buchwald 1994; Venanzoni and Gigante 2000; Ceschin and Salerno 2008; Lastrucci and Beccatini 2008; Mereu et al. 2012). On account of the floristic composition and ecology, we assigned the *C. stagnalis* stands to *Veronico beccabungae-Callitrichetum stagnalis*, a *Batrachion fluitantis* association found in streams, ditches, river edges and pools fed by springs or temporary waters, usually in shallow, stagnant to weak-flowing, meso- to eutrophic, clear and oxygenated waters, on sandy-gravelly to clayey bottoms, more or less rich in organic matter (Felzines 2016; Info Flora 2020).

The physiognomy of the observed stands is given by *C. stagnalis*, which at dry periods occurs in the typical form with floating, crowded rosettes covering large areas of the water surface; the species-poor coenosis contains also *Hippuris vulgaris*, *Ranunculus trichophyllus*, *Lemna trisulca* and the emergent *Veronica catenata*. It occurs along the margins of the major spring pools and of the larger brooks flowing from them (W sector), showing a tolerance to periodic exposed conditions. It forms dense bands in slow- to moderate-flowing, shallow, (oligo-) mesotrophic, clear spring waters in well-lit sites on silty beds. It is in contact with *Potamion pectinati* and *Batrachion fluitantis* communities of moderate-flowing waters, in particular with the *Hippuris vulgaris* community and *Potamo perfoliati-Ranunculetum fluitantis*; it is in contact also with emergent communities (esp. *Caricetum elatae* and *Schoenoplectetum lacustris*).

*Annex I Habitat (92/43/EEC Directive): 3260.*

**RANUNCULO TRICHOPHYLLI-CALLITRICHETUM POLYMORPHAE** Soó 1927 (Suppl. material 1, Table S5, rels 13–16)

The syntaxonomic treatment of communities dominated by *Callitriche cophocarpa* and *Ranunculus trichophyllus* is still rather critical. In this study the classification of this vegetation type follows Felzines (2016), who accepts the association *Ranunculo trichophylli-Callitrichetum polymorphae*, reporting it as a species-poor *Batrachion fluitantis* association dominated by *Callitriche cophocarpa*, fairly frequently accompanied by *Lemna minor* and *Ranunculus trichophyllus*, of shallow, slow-flowing to stagnant basic water. He attributes all the relevés of *Lemno-Callitrichetum cophocarphae* reported by Sburlino et al. (2008) from NE Italy to this association.

The physiognomy of the observed stands is determined by the large and soft masses of *C. cophocarpa* filling the water column; it can be present with the typical or the submerged form depending on the period of the year and the variation of the water level. The community is found in the springs area (W sector), in the upper and middle parts of the brooks fed by small limnocrenes, at short



distance from them, in small pools or stretches along the brooks with slow-flowing to almost standing waters at dry periods. It thrives in shaded sites within the *Salix alba* or *Ulmus minor* lakeshore woodland, in clear, oligo-mesotrophic, shallow water (30–60 cm deep at low-water), on silty bottoms partly with small stones. It tolerates shade conditions, and its ecological requirements appear rather similar to those of *Lemnetum trisulcae*. It is in contact with *Lemnetum trisulcae*, submerged *Potametea* communities, notably *Potamo perfoliati-Ranunculetum fluitantis* which is however related to higher light availability, and helophytic communities, especially *Caricetum elatae*.

*Annex I Habitat (92/43/EEC Directive): 3260.*

**CERATOPHYLLETUM DEMERSI** Corillion 1957 (Suppl. material 1, Table S6, rels 1–2)

At Doberdò *C. demersum* forms submerged, dense, almost monospecific stands, accompanied by a little *Elodea nuttallii*, found in the slow-flowing to almost standing waters of the major, deepest spring pools and swallow hole pools, respectively in the W and E sides of the lake basin, in different conditions of light and nutrient availability. Indeed, it occurs in the central parts of the two main spring pools in (oligo-)mesotrophic and rather transparent, clear water, being able to tolerate low levels of light as it represents the species that grows deeper into the water, reaching the bottom areas at a depth of up to 6 meters at low-water, where spring water outflows from the underground. Moreover, the community fills up the central part of the main swallow hole pool, 4 m deep at low water, in definitely eutrophic, turbid waters. It is in contact with submerged *Potamion* communities of slow-moving waters; in the main swallow hole pool it is surrounded by a belt of *Nymphaeetum albo-luteae* that grows in shallower waters.

*Annex I Habitat (92/43/EEC Directive): 3150.*

#### **PIONEER VEGETATION OF ANNUAL HYGRO-NITROPHILOUS HERBS (CLASS BIDENTETEA TRIPARTITAE)**

**POLYGONETUM HYDROPIPERIS** Passarge 1965 (Suppl. material 1, Table S7, rels 1–9)

The classification of the stands dominated by *Persicaria hydropiper* and *Bidens frondosa* found at Doberdò follows Šumberová (2011b). This community of tall annual hygro-nitrophilous and weed herbs occurs with two physiognomic aspects, dominated respectively by *Persicaria hydropiper* (rels 1–6, group 1 in Fig. 5) and *Bidens frondosa* and *Persicaria dubia* (rels 7–9, group 13 in Fig. 5); other diagnostic species occurring in both aspects are *Persicaria minor* and the exotics *Bidens vulgata* and *Xanthium italicum*. The community also contains many perennial elements of *Phragmito-Magnocaricetea* and *Agrostietea stoloniferae* which show the contact with marsh communities and perennial hygro-nitrophilous meadows. *Polygonetum hydropiperis* thrives in open sites on damp to waterlogged, silty-clayey eutrophic soils subject to frequent and high

water level fluctuation and exposed during the summer. It rapidly invades in late summer-autumn the muddy edges of the water bodies produced by the periodic water level oscillations, which in spring appear without vegetation. It is also found filling the open bare spaces within other perennial communities of the lake floor and its lower banks, and may invade them building up a dense, overtopping upper layer: this peculiar situation, promoted by the water regime of the karst lake, was interpreted as a seasonal overlap of an annual community on perennial ones.

The *Persicaria hydropiper* aspect colonizes the areas directly affected by the stream-phase dynamics (related to fluctuations during low-water phases), occurring along the fringes of the middle and lower course of the main stream and of the pools in the central and eastern sector, on substrates frequently covered by silty deposits brought by the rising of the water. It forms along the main stream a belt between the open water or the *Persicaria amphibia* community and the emergent communities such as *Caricetum elatae*, *Leersietum oryzoidis*, *Phragmitetum australis*; it is also found in seasonal overlapping on perennial *Phragmito-Magnocaricetea* communities (*Caricetum elatae*, *Leersietum oryzoidis*, *Eleocharitetum palustris*, *Persicaria amphibia* f. *terrestre* community). The aspect dominated by *Bidens* spp. and *Persicaria dubia* best grows along the lower parts of the lake-phase banks, in open or lightly shaded sites close to the lakeshore woods and scrubs, often in seasonal overlapping on *Potentillion anserinae* communities. Compared to the *Persicaria hydropiper* aspect it occurs in more landward or slightly more raised sites, inundated when the water body becomes a lake, on soils that are longer exposed and more subject to drying out in summer, somehow richer in nutrients. It is in contact waterward with the *Phragmito-Magnocaricetea* communities that cover the lake bottom, esp. *Caricetum elatae* and *Phragmitetum*, landward with *Potentillion anserinae* wet meadows and the lakeshore *Galio-Salicetum albae* and *Rhamno-Ulmetum minoris* woods.

*Bidens frondosa* is considered invasive in Italy and Europe and tends to displace the native *Bidens tripartita* (Banfi and Galasso 2010; Galasso et al. 2018; CABI 2020). Indeed, previous studies of the lake reported only the native *B. tripartita* (Vascotto 1967; Poldini 1989), never found in this survey.

*Annex I Habitat (92/43/EEC Directive): 3270.*

#### **PIONEER AMPHIBIOUS VEGETATION OF ANNUAL SMALL AND MEDIUM HERBS (CLASS ISOËTO-NANOJUNCETEA)**

**CYPERUS FUSCUS** community (Suppl. material 1, Table S7, rels 10–11)

Small stands made up of clumps of the short therophyte *C. fuscus* and few annual and perennial species were observed in the study area. The floristic composition agrees with *C. fuscus* stands reported from the banks of water bodies of central Italy, included in *Nanocyperion flavescentis*: they are a pioneer, ephemeral vegetation



of muddy water margins exposed and drying out during the summer favoured by frequent disturbance and remodeling of banks due to water level fluctuations (e.g. Venanzoni and Gigante 2000; Ceschin and Salerno 2008; Lastrucci et al. 2012, 2015). The observed community also contain elements of *Phragmito-Magnocaricetea*, *Bidentetea*, and *Agrostietea stoloniferae* (*Ranunculus repens*, *Agrostis stolonifera*, *Rorippa sylvestris*) and grows on the muddy banks of one of the two main spring pools and of the main swallow hole pool, on heavy silty-clayey soil that is exposed in the dry periods but remains damp. The sites are prone to high levels of disturbance, being frequently flooded, even by small rising of water level, and subject to intense trampling by animals, hikers and visitors. The community is in contact with *Potametea* coenoses, the emergent *Persicaria amphibia* community, *Caricetum elatae* and *Potentillion anserinae* vegetation.

*Annex I Habitat (92/43/EEC Directive):* 3130.

### FRESHWATER MARSH VEGETATION (CLASS PHRAGMITO-MAGNOCARICETEA)

*SCHOENOPLECTETUM LACUSTRIS* Chouard 1924 (Suppl. material 1, Table S8, rels 1–9)

This is the community that is able to extend out in deeper water than the other helophyte coenoses, often representing the first emergent vegetation between the open water and other communities of the banks. Compared to the other reed communities it is able to tolerate shorter periods of exposed soil that occur at longer intervals (Pott 1995; Šumberová et al. 2011; Landucci et al. 2013).

At Lake Doberdò *Schoenoplectus lacustris* stands are often rather sparse and species-poor. The community is rather common and can be found in three main different situations: a) the almost standing waters of the edges of the main spring and swallow hole pools where it forms scattered narrow bands (rels 1–2); b) a wide area of the central-eastern sector that is permanently flooded or at least waterlogged all year round (rels 3–5); c) areas adjacent to the main stream or shallow depressions of its floodplain (i.e. the exposed lake floor) that are not submerged during low-water periods but are prone to long, periodic flooding or have heavily saturated soils; here the coenosis is found as small scattered stands in mosaics with other marshy communities (rels 6–9). These situations correspond to two main aspects of the community. One aspect (rels 1–5) includes species-poor stands dominated by *S. lacustris* occurring in permanently submerged or waterlogged zones; in the water at the base of the stems of *S. lacustris* aquatic species can be found (such as *Lemna minor*, *Myriophyllum spicatum*). The other aspect (rels 6–9), richer in species, occurs in only periodically flooded stands, subject to larger variations of the water level and soil moisture, where the helophytes *Carex elata* and/or *Eleocharis palustris* become more abundant, forming a second layer of vegetation below the stems of *S. lacustris*; however, tussocks of *C. elata* are here more scattered than

in the *Caricetum elatae* association. A previous study of the lake vegetation (Vascotto 1967) reveals that the last situation represents what remains of a former, much wider distribution of *Schoenoplectetum lacustris*, which in the 1960s covered very large areas. The marked change of the distribution of the community can be attributed to a modification of the water regime of the karst lake, and *Schoenoplectetum lacustris* can be considered in dynamic contact at local level with *Phragmitetum australis* and *Caricetum elatae*. It is in catenal contact with the same coenoses in sites with lower or more varying water level, waterward with aquatic *Lemnetea* and *Potametea* communities.

*Annex I Habitat (92/43/EEC Directive):* -.

*PHRAGMITETUM AUSTRALIS* Savič 1926 (Suppl. material 1, Table S8, rels 10–16)

*Phragmitetum australis* has a very broad ecological amplitude, being found along the edges of a wide range of habitats of standing and flowing, mesotrophic to eutrophic, fresh or brackish waters, in deep water to intermittently flooded or not flooded sites, showing a high tolerance to dry conditions (Preston and Croft 1997; Šumberová et al. 2011; Landucci et al. 2013, 2020). It is a typical community of the infilling process of water bodies and it tends to increase in extent during the turning of a lake into a marsh.

In the study area the association occurs with extensive, species-poor, dense stands of *Phragmites australis* often accompanied by a little *Lysimachia vulgaris*, *Lythrum salicaria* and *Persicaria amphibia* f. *terrestre*. In more flooded sites *Schoenoplectus lacustris* joins the common reed, while in some marginal sites, subject only to periodic inundations, a facies with *Carex elata* is found (rels 15–16). There are also stands with a clear two-layer structure, formed by dense tussocks of *C. elata* under the beds of *P. australis*, which are interpreted as a transitional stage of interpenetration of *Phragmitetum australis* with *Caricetum elatae*. Common reed beds cover a large part of the basin (ca. 1/4). Three main aspects of the coenosis can be distinguished, which correspond fairly well to some variants identified by Lastrucci et al. (2017b): a) a wet, monospecific aspect of sites permanently submerged by shallow waters in the dry periods, corresponding to the variant “*nudum*” (rel. 10); b) a wet aspect, close to the variant with *Lythrum salicaria*, on soils that tend to emerge in the dry periods but remain waterlogged or slightly submerged (rels 11–14); c) an aspect with *Carex elata*, not observed by Lastrucci et al. (2017b), on soils that tend to dry out at low-water periods but still damp, with a more amphibious/dry character (rels 15–16).

Comparison with past data (Vascotto 1967) highlights the expansion of *Phragmitetum* to the detriment of *Schoenoplectetum lacustris* and *Caricetum elatae*. Furthermore, transitional stands made up of *P. australis* invading former *Caricetum elatae* areas have appeared (see comment to *Caricetum elatae*). The increasing occurrence of *Phragmites australis* shows that in the study area common



reed beds are not affected by the progressive decline observed in many areas of Europe and recently in Italy as well (e.g. Den Hartog et al. 1989; Ostendorp 1989; Brix 1999; Gigante et al. 2013). The literature evidences that the widespread phenomenon of reed die-back may be the effect of several natural and human-induced causes (e.g. Van der Putten 1997; Gigante et al. 2014; Leuschner and Ellenberg 2017). The observed expansion of reed beds at Lake Doberdò in the last 50 years can be connected to two main factors. One is the natural process of lake infilling, promoted by the lack of management that was once maintained by the regular mowing of marsh vegetation, in particular of *P. australis* and *Carex elata*, and was gradually abandoned after the Second World War. The change in the distribution of reed beds could be also correlated with a modification of the hydrologic regime of the karst lakes system, as a result of direct or indirect impacts of human actions and climate changes, which is leading to a drying up of the wetland. Indeed, most stands of *Phragmitetum australis* in the study area are not permanently and deeply submerged, corresponding to the aspects less affected by die-back according to the findings of Lastrucci et al. (2017b). In several areas, the recruitment of *Salix cinerea*, *S. purpurea* and *Amorpha fruticosa* demonstrates an ongoing encroachment process of *Phragmitetum australis*, which represents a further step of the natural succession connected to lake infilling and abandonment of management. The community is in dynamic contact with *Schoenoplectetum lacustris*, *Caricetum elatae* and *Frangulo-Salicetum cinereae*. It is in catenal contact along the water edges with *Potametea* vegetation of still or slow-flowing waters, landward with the *Salix cinerea* scrubland, and along the lower lake banks with hygro-nitrophilous annual and perennial vegetation (*Bidentetea tripartitae* and *Agrostietea stoloniferae*), *Galio-Salicetum albae* and *Rhamno-Ulmetum minoris* woodland.

*Annex I Habitat (92/43/EEC Directive): -.*

*TYPHETUM LATIFOLIAE* Nowiński 1930 (Suppl. material 1, Table S8, rel. 17)

*Typha latifolia* generally grows in shallow waters or exposed mud, frequently being replaced by *Phragmites australis* in deeper water, the latter species being a much stronger competitor if water levels are high (see Leuschner and Ellenberg 2017). It is very tolerant of eutrophication, anoxic soil conditions and drying out in the summer, although being more sensitive to dry conditions than *Phragmites australis* (Preston and Croft 1997; Šumberová et al. 2011; Landucci et al. 2013, 2020).

At Lake Doberdò the community was found as few small scattered stands of *T. latifolia* accompanied, among others, by *Carex elata*, *C. vesicaria*, *Leersia oryzoides* and *Mentha arvensis*. Structure and accompanying species reveal a terrestrialization aspect of the community, which occurs on the exposed mud of the banks of the main spring pools and brooks, in open sites frequently flooded but otherwise damp and subject to drying for several months during the year, in definitely less wet situations

compared to *Schoenoplectus* and *Phragmites* beds. The very limited distribution of the coenosis could be linked to the relationship of *Typha* beds with small water-level fluctuation and nutrient-enrichment conditions (Albert and Minc 2004). It is in contact with helophytic communities, notably *Caricetum elatae* and *Caricetum vesicariae*, and *Glycerio-Sparganietum neglecti* growing along the edges of the spring channels.

*Annex I Habitat (92/43/EEC Directive): -.*

*IRIDETUM PSEUDACORI* Eggler ex Brzeg & Wojterska 2001 (Suppl. material 1, Table S8, rels 18–20)

At Lake Doberdò *Iridetum pseudacori* is found as almost monospecific dense stands of limited size of *Limniris pseudacorus*, often accompanied by *Carex elata*, *Lysimachia vulgaris*, *Lythrum salicaria* and *Mentha arvensis*. It grows in open sites along the edges of the spring pools, their brooks and the main stream, mainly in the W and central sectors, on muddy soils flooded or damp for most part of the year but exposed during dry periods; it often occurs in shallow depressions of the ground. It is found in mosaics with other *Phragmito-Magnocaricetea* communities, namely *Schoenoplectetum lacustris*, *Caricetum elatae*, *Glycerio-Sparganietum neglecti* and the *Persicaria amphibia* community; towards the lower lake banks it is in contact with *Bidentetion tripartitae* and *Potentillion anserinae* hygro-nitrophilous communities.

*Annex I Habitat (92/43/EEC Directive): -.*

*GLYCERIO-SPARGANIETUM NEGLECTI* Koch 1926 (Suppl. material 1, Table S8, rels 21–24)

Stands dominated by *Sparganium erectum* s.l. occur in shallow, standing or slow-flowing waters in water bodies in advanced phases of infilling and drying out or lentic sections of watercourses; they are found in mesotrophic to eutrophic waters, also with a layer of organic sediments on the bottom, on fine, often anoxic soils (Venanzoni and Gigante 2000; Šumberová et al. 2011; Landucci et al. 2013).

At Doberdò the community is restricted to the spring area (W sector). It is found as dense, almost monospecific narrow dense bands of *S. neglectum* along the banks of the lower course of the smaller spring brooks and flanking the major brooks, both in open and partially shaded areas within the lakeshore *Salix alba* wood. It grows in slow-running to almost standing, mesotrophic spring waters, on muddy substrates that are permanently wet or at least waterlogged in the dry periods. It is generally found in shallow waters, 10–20 cm deep at low-water periods. The community is extensively colonizing the channel of the spring brooks, promoting their infilling thanks to the vigorous growth of *S. neglectum*. It is in contact on the water side with communities of standing or slow-running waters (notably *Potametum lucentis*, *Parvopotamo-Zannichellietum palustris*, *Ranunculo-Callitrichetum polymorphae*), along the brook banks with *Beruletum erectae*, landward with *Caricetum elatae* and the lakeshore willow scrubs and woods.

*Annex I Habitat (92/43/EEC Directive): -.*



*PHALARIDETUM ARUNDINACEAE* Libbert 1931 (Suppl. material 1, Table S8, rels 25–28)

In its original circumscription, *Phalaridetum arundinaceae* occurs in lentic sites subject to regular and strong but slow water level fluctuations, not directly affected by mechanical effects of the water current, on wet soils with prevailing fine particles and accumulation of organic matter; it differs from *Rorippo-Phalaridetum arundinaceae*, a more eutrophic *Phalaris arundinacea*-dominated community related to flowing waters found in river sites usually directly disturbed by the current and floods on sandy-clayey to gravelly substrates (Balátová-Tuláčková et al. 1993; Šumberová et al. 2011; Landucci et al. 2013). Recently Landucci et al. (2020) merged the two associations into a single one (*Phalaridetum arundinaceae*), assigned to *Phragmition communis*.

In the *Phalaris arundinacea*-stands of Lake Doberdò the typical elements of the class *Phragmito-Magnocaricetea* predominate; there are some annual hygro-nitrophytic species (*Bidens frondosa*, *Xanthium italicum*), which however occur as sporadic or with low cover, while definitely nitrophytic, ruderal species of *Galio-Urticetea* are absent. The coenosis therefore shows the features of *Phalaridetum arundinaceae* in its original meaning. It occurs as small patches in areas adjacent to the main brooks and the upper course of the main stream, in the SW sector near the springs. It is found in sites slightly distant from the water, not directly affected by water current dynamics, which are frequently flooded by slow water level fluctuations, denoting a lentic character, on muddy soils that are exposed in the dry periods but remain damp. It may occur as small, open stands in complexes of marsh communities of *Phragmito-Magnocaricetea*, in particular of *Magnocaricetalia* (esp. *Caricetum elatae*, *Caricetum vesicariae*, *Leersietum oryzoidis*), but it is more often found as the fringe of the *Salix cinerea* scrub or the *Salix alba* wood.

*Annex I Habitat* (92/43/EEC Directive): -.

*CARICETUM ELATAE* Koch 1926 (Suppl. material 1, Table S9, rels 1–16)

This is the marsh community that tolerates the largest variations of water level, found in shallow, calcareous, mesotrophic to eutrophic waters at the edges of lakes, ponds, canals and in river floodplains, requiring a regime of remarkable, periodic and long-lasting flooding, with water level remaining few centimeters below the ground surface in summer (Balátová-Tuláčková 1968; Šumberová et al. 2011).

At Doberdò the community occurs in its typical aspect, a species-poor marsh vegetation dominated by the characteristic tussocks of *Carex elata*. In the muddy spaces among the tussocks various marsh species grow: *Lythrum salicaria* and *Lysimachia vulgaris* are common and at the base of the tussocks the moss *Fontinalis antipyretica* may be often found. Landward stands are characterized by the occurrence of *Leucojum aestivum*, its presence in the *Carex elata* vegetation being here related to the slight

shading given by the proximity of the lakeside woods, indicating shade facies of *Caricetum elatae*.

Together with *Phragmitetum australis*, it is the most widespread community of the lake, found in areas subject to higher water level variations. Stands in the central and eastern sectors, which are subject to more prolonged and stronger floods being located at the lowest elevations, are very wide in extent and quite typical in their floristic composition: the number of species is very low and aliens are not or almost not present. Conversely, in the western, slightly more elevated sector, the community is often found as small patches in mosaics with other marsh coenoses. Landward stands are richer in species but more affected by annual hygro-nitrophilous and exotic elements. The community is widespread in open sites but occurs also in light shaded areas within the lakeside woodland. It occurs with three main aspects: a) an aspect with *Lythrum salicaria*, found in the wettest, long flooded sites near the main stream and the pools in the E sector on soils that emerge only in the driest periods but remain waterlogged: it includes species-poor stands where *C. elata* is overtopped by dense *Lythrum salicaria* that intensely colours these areas purple during the summer, accompanied by little *Schoenoplectus lacustris* (rels 1–4); b) a typical, slightly less wet aspect (rels 5–9), with a monotonous physiognomy given by *C. elata*, which may be accompanied by abundant *Persicaria hydropiper* in summer; c) a little drier aspect with *Lysimachia vulgaris* (rels 10–16), occurring on slightly raised or landward sites and enriched with more terrestrial elements indicating less wet conditions or the contact with the lakeside woods, such as *Leucojum aestivum*, *Carex vesicaria*, *Galium palustre* subsp. *elongatum*; alien hygro-nitrophilous species (esp. *Bidens frondosa*) are here more frequent. Stands with *Carex vesicaria* are rather common along the lake banks (rels 13–16), and could be related to *Caricetum elatae caricetosum vesicariae* Balátová-Tuláčková 1976. Along the banks of the spring brooks *Potentillion anserinae* elements increase (e.g. *Ranunculus repens*, *Potentilla reptans*, *Thalictrum lucidum*) (rel. 16).

Compared to the 1960s (Vascotto 1967) the community has considerably spread mainly to the detriment of the aquatic vegetation and *Schoenoplectetum lacustris*. This is consistent with a change of the hydrological regime and an ongoing filling process of the lake. On the other hand, some former areas of *Caricetum elatae* are being invaded by *Phragmites australis*, possibly as a consequence of abandonment of regular mowing of the tufted sedge marshes and reed beds and a further phase of hydrological changes: these situations are attributable to *Caricetum elatae phragmitetosum australis* Gerdol 1988. The same tendency of *Caricetum elatae* to decrease in size and to be often substituted by the common reed is recorded from central Italy by Lastrucci et al. (2017a), who attribute this process to habitat loss or degradation or the abandonment of traditional activities of chair stuffing. The community is in contact with *Caricetum vesicariae* and other helophytic communities (e.g., beds of *Schoenoplectus lacustris*,



*Phragmites australis*, *Sparganium neglectum*, *Leersia oryzoides*, *Persicaria amphibia*) and *Polygonetum hydropiperis*. Waterward it is in contact with *Potametea* communities, landward with *Potentillion anserinae* wet meadows, *Frangulo-Salicetum cinereae*, *Galio-Salicetum albae* and the meso-hygrophilous *Rhamno-Ulmetum minoris*.

*Annex I Habitat (92/43/EEC Directive): -.*

**CARICETUM VESICARIAE** Chouard 1924 (Suppl. material 1, Table S9, rels 17–23)

*Caricetum vesicariae* grows in shallow marshes, at the edges of lakes, ponds and pools, and depressions that are waterlogged permanently or for most of the year. Water level and soil moisture may be subject to considerable fluctuations and the soil may dry out during the summer, with the water table dropping much deeper than *Caricetum elatae*; however dry conditions are tolerated only for short time and the coenosis demands high soil moisture. It occurs on mesotrophic to eutrophic, mineral and/or partly organic (anmoor) soils, rich in silt, often in light shade, being on the whole more eutrophic than *Caricetum elatae* (Balátová-Tuláčková et al. 1993; Buchwald 1994; Šumberová et al. 2011; Landucci et al. 2013).

At Lake Doberdò the community occurs as species-poor, often almost pure uniform meadows of *Carex vesicaria* (rels 17–21). It covers some large landward open areas near the main spring pools and a swallow hole pool; moreover it occurs as more or less broad, well-detectable patches in mosaics with other marsh coenoses in the slightly more elevated part of the basin, always in contact with *Caricetum elatae*. *Caricetum vesicariae* also covers the lower parts of the channel of some small spring-fed brooks in shaded sites (rels 22–23). Compared to *Caricetum elatae*, it is found in sites with a greater amount of organic sediments, often slightly more raised and subject to more prolonged emersion. It has never been reported from the study area or the Italian Karst (Vascotto 1967; Poldini 1989, 2009). Its present distribution denotes a change in the ecological characteristics of the karst lake occurred in the last decades. The spread of the coenosis over mainly landward areas formerly covered by *Caricetum elatae* may have been driven by a change of the water level regime, due to a reduction in duration and frequency of floods, and a natural input of silt and organic sediment in the marginal areas of the lake, caused by the transportation by water flow and the accumulation of organic matter due to the dynamic changes of the surrounding vegetation, resulting in the development of scrubland and woodland. Indeed, *Caricetum vesicariae* can be found in light shaded sites near the edges of lakeside woods, where the supply of organic matter is higher, as observed by Stančić (2010). The occurrence of the community on the wet soils of the channel of small watercourses can be promoted by the nature of the soil, characterized by higher silt and organic fractions. It is in catenal contact with *Caricetum elatae*, *Phalaridetum arundinaceae*, hygro-nitrophilous *Bidentetea* and *Agrostietea stoloniferae* communities and the

lakeshore *Galio-Salicetum albae*; in small watercourses it is also in contact with submerged *Potametea* vegetation.

*Annex I Habitat (92/43/EEC Directive): -.*

**BERULETUM ERECTAE** Roll 1938 (Suppl. material 1, Table S10, rel. 1)

*Berula erecta* stands are found in watercourses, in mesotrophic, well-oxygenated, calcareous waters with high or low current speed (Landucci et al. 2013). The treatment of *B. erecta* coenoses is controversial in the literature (see e.g. Sburlino et al. 2008; Šumberová et al. 2011; Landucci et al. 2013, 2020; Mucina et al. 2016). The association is here assigned to *Phragmito-Magnocaricetea*, although maintaining the autonomy of *Beruletum erectae* from the aquatic *Ranunculo trichophylli-Sietum submersi* (see comment to *Potamo-Ranunculetum fluitantis*); in accordance with Sburlino et al. (2008) we point out that the submerged, almost monospecific *Berula erecta*-stands are a typical vegetation of the upper stretches of small brooks close to their springs, found both in shaded or well-lit situations in correspondence with the karstic small limnocrenes and the resurgence belt of the nearby plains of NE Italy.

In the study area the community occurs as species-poor stands dominated by *Berula erecta*: during the dry periods the species occurs in a partially submerged to almost emergent form, but it is completely submerged in middle- or high-water periods, being subject to strongly variable conditions of submersion during the year. *Beruletum erectae* is restricted to a small, spring-fed brook in the NW sector, where it colonizes the bed and the banks of shaded stretches within the *Ulmus minor* and *Populus nigra* wood; it grows in slow-running, shallow (10–30 cm deep at low-water periods), (oligo-)mesotrophic, clear spring water, on stony-silty substrates but it flourishes best on silty bottom. It is in contact waterward with *Lemnetum trisulcae* and *Hippuris vulgaris* f. *fluviatilis* community, along the brook banks with *Caricetum elatae* and *Glycerio-Sparganietum neglecti*.

*Annex I Habitat (92/43/EEC Directive): -.*

**ELEOCHARITETUM PALUSTRIS** Savič 1926 (Suppl. material 1, Table S10, rels 2–4)

At Lake Doberdò this pioneer community consists of species-poor stands dominated by *Eleocharis palustris*, accompanied by hygrophilous species such as *Carex elata*, *Leersia oryzoides*, *Lythrum salicaria*, *Schoenoplectus lacustris*, along with hygro-nitrophilous elements such as *Galium palustre* subsp. *elongatum*, *Gratiola officinalis*, *Mentha arvensis* (rel. 4) present especially towards the lake banks. In spring the physiognomy of the community is given by the sparse stems of *E. palustris* colonizing the bare muddy soils; as the summer goes by, the community can be completely overwhelmed by annual *Bidention* weeds dominated by *Persicaria hydropiper* and *Bidens frondosa*. It thrives in the muddy areas closest to the water that are frequently disturbed by water level fluctuations and exposed in dry periods: it colonizes some stretches of the banks of the upper and middle course of the main



stream in the W sector, and the edges of the swallow hole pools in the N and E sectors. It is found as small patches in mosaics with *Caricetum elatae*, the *Persicaria amphibia* community and other *Phragmito-Magnocaricetea* coenoses, often in seasonal overlap with annual *Bidentetea* communities. Towards the water it is in contact with submerged *Potametea* communities of stagnant or slow-flowing waters, landward along the lake edges with *Potentillion anserinae* wet meadows.

*Annex I Habitat (92/43/EEC Directive): -.*

**PERSICARIA AMPHIBIA** F. TERRESTRE community (Suppl. material 1, Table S10, rels 5–15)

*Persicaria amphibia* is able to grow both as an aquatic and a terrestrial plant, often as large pure clonal colonies thanks to its far-creeping rhizomes, and is tolerant of strong water level fluctuations and turbidity. Stands dominated by the terrestrial form are well defined from the ecological point of view, although they have not yet been described at the association level: they constitute a pioneer amphibious vegetation on muddy and clayey soils submerged for most of the year and exposed in the dry periods. Such vegetation is reported from central Italy in karst and alluvial plains, ponds and swamps (Landucci et al. 2013).

The observed stands perfectly agree with the emergent *P. amphibia* community outlined by Landucci et al. (2013). In spring the community consists of almost pure, dense to sparse stands of *Persicaria amphibia*, accompanied by few perennial elements such as *Leersia oryzoides*, *Carex elata*, *Schoenoplectus lacustris*. During the summer the hygro-nitrophilous weeds *Persicaria hydropiper*, *Bidens frondosa* and *Xanthium italicum* appear and may invade the stands close to the main stream building up a dense upper layer of plants (rels 12–13): this situation was interpreted as a seasonal overlap of the annual *Polygonetum hydropiperis* on the perennial *Persicaria amphibia* community. A facies with abundant *Lysimachia vulgaris* (rels 14–15) was observed in areas more distant from the main stream. Conversely, in water edge sites the presence of *Nuphar lutea*, *Myriophyllum spicatum* and *Ranunculus trichophyllus* highlights the contact with aquatic communities of standing or slow-flowing waters. *P. amphibia* is particularly favoured by the typical water regime of the karst lake. The emergent coenosis colonizes the shallow, standing or slow-flowing, mesotrophic to eutrophic, often turbid waters and the damp muddy edges of the middle and lower course of the main stream and of the swallow hole pools, in the central and E sectors, growing in sites subject to frequent disturbance due to the periodic rising of the water and enriched in fine mineral and organic sediment deposited by the water flow. Here *P. amphibia* stands are rather sparse, forming narrow bands along the edges of the stream and wider stretches along the more gently sloped banks of the pools (rels 5–11). Dense stands cover quite large areas of the floodplain (i.e. the exposed lake floor) along the middle course of the main stream, on permanent damp soils that are exposed for long peri-

ods (rels 12–15). The coenosis shows a remarkable resistance also to trampling and rooting due to animals, here in particular wild boars. It is in contact waterward along the main stream with *Potamion* communities, at the pools also with *Nymphaeion* and *Ranunculion aquatilis* communities, landward with *Polygonetum hydropiperis*, *Caricetum elatae* and *Phragmitetum australis*.

*Annex I Habitat (92/43/EEC Directive): -.*

**LEERSIETUM ORYZOIDIS** Eggler 1933 (Suppl. material 1, Table S10, rels 16–24)

Corr. name: “fitocenon a *Leersia oryzoides*” in Poldini (1989)

This thermophilous wet grassland typical of muddy, nutrient-rich soils is found in shallow littoral zones with periodical changes of water level and exposed during the dry periods of rivers, lakes and ponds, or in intermittently flooded sites in floodplains. It requires permanently saturated soils as it does not tolerate marked desiccation, but it cannot tolerate prolonged flooding by water more than few centimeters deep during the growing season (Šumberová et al. 2011; Landucci et al. 2013).

The most common elements of the observed community mainly belong to the class *Phragmito-Magnocaricetea*, and include also the annuals *Bidens frondosa* and *Persicaria hydropiper*. The *Leersia oryzoides* wet meadows are rather common, but cover rather small areas, located mainly in the central and eastern part of the basin, along the margins of the watercourses, of the swallow hole pools and of the lake floor. The community grows on muddy soils temporary flooded but remaining damp during the summer, subject to silty sediment deposition and nutrient-enrichment due to frequent flooding. In more sparse stands, annual hygro-nitrophilous plants quickly colonize during the summer the bare muddy spaces determined by the periodic flooding. Two aspects of the association can be recognized. One (rels 16–19, group 2 in Fig. 5) corresponds to wetter stands, adjacent to the watercourses and the swallow hole pools, characterized by the disappearance of the less hygrophilous elements, a reduction of species number and the extensive development during the summer of *Persicaria hydropiper*, which can give rise to situations interpreted as a seasonal overlap of the annual *Polygonetum hydropiperis* on the perennial *Leersietum*. The second aspect (rels 20–24, group 4 in Fig. 5) comprises stands found in the less inundated marginal parts of the lake floor, characterized by species such as *Agrostis stolonifera*, *Galium palustre* subsp. *elongatum*, *Mentha arvensis*, *Lysimachia vulgaris*, many of which belonging to *Agrostietea stoloniferae*. Rel. 24 represents a peculiar aspect with abundant *Mentha arvensis*, which shows features somehow analogous to *Teucrio scordii-Menthetum arvensis*, a mesotrophic *Agrostietea stoloniferae* meadow association reported from temporarily long flooded, weakly trampled areas bordering ponds or lakes of NE France (Villaumé and Tournebize 2011; de Foucault and Catteau 2012). *Leersietum* is found in mosaics with *Caricetum elatae* and other *Phragmito-Magnocaricetea* co-



enoses, notably the *Persicaria amphibia* community and *Eleocharitetum palustris*; it is in contact landward also with *Phalaridetum arundinaceae*, *Frangulo-Salicetum cinereae* and *Galio-Salicetum albae*.

*Annex I Habitat (92/43/EEC Directive): -.*

#### PERENNIAL HYGRO-NITROPHILOUS VEGETATION OF WET MEADOWS (CLASS AGROSTIETEA STOLONIFERA)

These communities are spread in the lower parts of the lake banks that are regularly flooded at the normal high-water phases of the lake.

*GRATIOLA OFFICINALIS* community (Suppl. material 1, Table S11, rels 1–4)

This species-poor and fairly dense low herbaceous vegetation is dominated by *Gratiola officinalis*: various perennial creeping species occur, such as *Potentilla reptans*, *Ranunculus repens* while annuals are almost absent. *G. officinalis* is considered an element generally occurring in *Molinion* wet meadows, but, on account of the clear prevalence of *Potentillion anserinae* species and the ecology, the community is attributed to this alliance, as done by Lastrucci and Beccattini (2008) for similar *G. officinalis*-dominated vegetation from the banks of some wetlands in Tuscany. The community occurs as small stands in shallow depressions on waterlogged, silty-clayey, eutrophic to strongly eutrophic muddy soils that are frequently and long flooded by shallow, stagnant, turbid water and remain wet during the summer, located near the main swallow hole pools in the NE and E margins of the lake. It represents the wettest aspect of the *Potentillion anserinae* coenoses of the survey area. It is found in contact waterward with *Eleocharitetum palustris* and *Caricetum elatae*, landward with other *Potentillion anserinae* coenoses, in particular with *Ranunculetum repentis*.

*Annex I Habitat (92/43/EEC Directive): -.*

*RANUNCULETUM REPENTIS* Knapp 1946 (Suppl. material 1, Table S11, rels 5–7)

At Doberdò, this low perennial herbaceous community dominated by *Ranunculus repens* is found as stands often rather small in size and generally not very dense, but during the summer the community is invaded by annual tall-growing *Bidentetea* and exotic elements (*Persicaria dubia*, *Ambrosia artemisiifolia*, *Bidens frondosa*, *Xanthium italicum*). Similar *Ranunculus repens*-dominated communities are reported from central Italy along river banks and attributed to this association (e.g. Baldoni and Biondi 1993; Pirone et al. 2003; Mereu et al. 2012). The ecology and distribution of this vegetation are similar to those of the *Potentilla reptans* community, although *Ranunculetum repentis* grows in slightly more waterward, damper and more muddy sites, often forming a transitional strip between the marshy *Caricetum elatae* and the wet perennial *Agrostis stolonifera* meadows. It is found along the NE and E lake edges, which in the past were subject to livestock pressure. It is in contact laterally with the *Potentilla*

*reptans* community, on damper soils with *Gratiola officinalis* community, waterward with *Caricetum elatae* and *Caricetum vesicariae*, landward with *Rorippo-Agrostietum* and the *Salix alba* wood; it can be in seasonal overlapping with *Polygonetum hydropiperis*.

*Annex I Habitat (92/43/EEC Directive): -.*

*POTENTILLA REPTANS* community (Suppl. material 1, Table S11, rels 8–11)

The community includes stands dominated by *Potentilla reptans*, accompanied by *Agrostis stolonifera* and other hygro/meso-hygrophilous species such as *Gratiola officinalis*, *Rorippa sylvestris*, *Rumex conglomeratus*. In summer it also contains annual tall-growing *Bidention* elements. It colonizes the silty-clayey, nutrient-rich soils of the lower parts of the lake banks, which are much subject to waterlogging due to periodic floods. It is typically found in eutrophic sites that are damper and more disturbed by the periodic raising of the lake water level compared to *Rorippo-Agrostietum*, but still exposed in the dry season. It is spread in the E sector of the study area, on the lake shores where water movements tend to accumulate both mineral and organic deposits and which were subject to livestock disturbance and passage of people in the 1960s. Both *Potentilla reptans* and *Ranunculus repens* are known to tolerate compacted, trampled soils; indeed the *P. reptans* community prevails on compacted, muddy soils of lakeside paths trampled by animals. It is often found in mosaics with *Rorippo-Agrostietum* or *Ranunculetum repentis*; it is in contact waterward with *Caricetum elatae* and landward with *Galio-Salicetum albae* and *Rhamno-Ulmetum minoris* woodlands; it can be in contact or in seasonal overlapping with *Polygonetum hydropiperis*.

*Annex I Habitat (92/43/EEC Directive): -.*

*RORIPPO SYLVESTRIS-AGROSTIETUM STOLONIFERA* Oberdorfer & Müller in Müller 1961 (Suppl. material 1, Table 11, rels 12–16)

This is a low meadow characterized by the dense cover of *Agrostis stolonifera*, accompanied by *Rorippa sylvestris*, a constant species usually occurring at Doberdò with low cover values; the community also contains *Teucrium scordium* subsp. *scordioides*, rare at the regional level. During the late summer the coenosis becomes invaded by *Bidens* and *Persicaria* species, which form a dense, upper layer consisting of the *Bidens*-dominated aspect of *Polygonetum hydropiperis*. This fringing, eutrophic to mesotrophic wet meadow related to clayey, poorly oxygenated rather compacted soils subject to periodic flooding (Poldini 1989) occurs as a narrow strip along the lower parts of the lake banks, mainly in the E and N sectors, representing the uppermost hygro-nitrophilous herbaceous community along the lake shore. In the past, this area used to be regularly trampled by livestock and there was a path used by local people bordering the lake (A. Scarpa, pers. comm.) It is found in mosaics or in contact slightly downwards with the wet meadows with *Potentilla reptans* and *Ranunculus repens*; downwards it comes also



in contact with marsh coenoses, in particular *Caricetum elatae*, *Phragmitetum australis*, landward with the *Rhamno-Ulmetum minoris* woodland; it can be in contact or in seasonal overlapping with *Polygonetum hydropiperis*.

*Annex I Habitat (92/43/EEC Directive): -.*

### FLOODED HAY MEADOWS (CLASS MOLINIO-ARRHENATHERETEA)

*LEUCOJO AESTIVI-POETUM PRATENSIS* Tasinazzo ex Castello, Poldini & Altobelli *ass. nov.* (Suppl. material 1, Table 12)

*Holotypus*: rel. 8 of Tab. 3 in Tasinazzo 2009: p. 42; Loc.: Prà dei Gai, Eastern Venetian Plain (NE Italy)

*Nomenclatural syn.*: *Leucojo aestivi-Poetum pratensis* *ass. prov.* Tasinazzo 2009 (Fitosociologia 46(2): 36) *nom. inval.* (art. 3b)

*Diagnostic species*: *Leucosium aestivum* subsp. *aestivum*, *Inula salicina*, *Ononis spinosa* subsp. *austriaca*, *Sanguisorba officinalis*, *Oenanthe pimpinelloides* (Tasinazzo 2009).

An interesting periodically flooded hay meadow lies on the NE bank of the lake. The physiognomy of the community is mainly given by *Poa pratensis*, *Bromus racemosus*, *Lychnis flos-cuculi* and *Oenanthe pimpinelloides*. The community is characterized by a considerable group of hygrophilous species typical of damp, oligo-mesotrophic *Molinietalia* coenoses and found also in *Trifolio-Hordeetalia* periodically flooded meadows of the central Apennine and Balkan karst basins. They join with *Potentillo-Polygonetalia* elements of wet, long-inundated meadows. The community occurs in the lower part of a gentle slope going down to the lakeshore, in sites with rather high water table and deep soils that are regularly flooded by high-water peaks for few days/weeks especially in spring and autumn, but in the summer the soil tends to dry; periodical floods determine a natural fertilization.

The coenosis shows remarkable affinities with two lowland communities reported from NE Italy, namely *Poo sylvicolae-Lolietum multiflori leucojetosum aestivi*, including *Arrhenatherion* wet hay meadows and water meadows of the Low Po Plain that are sometimes moderately manured and characterized by a high incidence of hygrophilous elements of *Molinietalia* and *Potentillion anserinae* (Poldini and Oriolo 1995), and *Leucojo aestivi-Poetum pratensis*, provisionally described by Tasinazzo (2009), being known only from a single locality, from a wet area of the E Venetian Plain as a wet *Molinion* coenosis spread in depressions close to the Livenza and Rasego rivers subject to the influence of the high water table and episodic flooding.

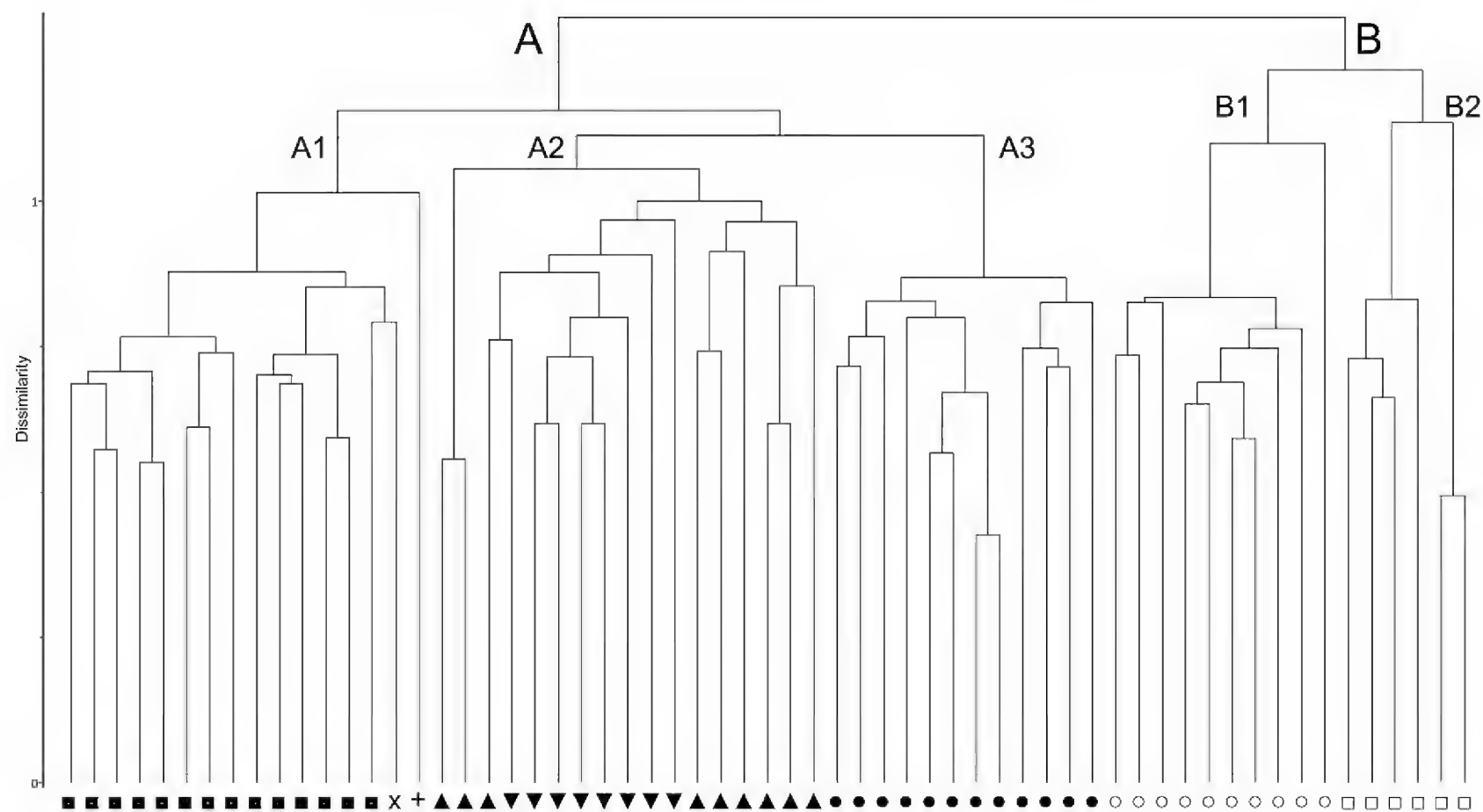
The relevé of the hay meadow from Lake Doberdò was compared with the original analytic tables of the two coenoses from Poldini and Oriolo (1995) and Tasinazzo (2009), of other lowland *Arrhenatherion* and *Molinion* communities found in NE Italy, namely the lowland relevés of *Centaureo carniolicae-Arrhenatheretum elatioris* from Poldini and Oriolo (1995), *Plantagini altissimae-Molinietum caeruleae* from Marchiori and Sburlino (1982) and *Serratulo-Plantaginetum altissimae*

from Poldini (1989), along with an unpublished relevé of a wet riverside hay meadow from a lowland protected area along the border between Veneto and Friuli (Palù di Settimo). The cluster analysis (Fig. 6) separates the relevés in two main groups. Group A gathers the stands of *Leucojo-Poetum*, the stands from Lake Doberdò and Palù, and those of the *Arrhenatherion* communities of *Poo-Lolietum multiflori* and *Centaureo-Arrhenatheretum elatioris*. Subcluster A1 groups *Leucojo-Poetum* stands and those from Lake Doberdò and Palù, corresponding to wetter and periodically flooded meadows along water bodies. They are clearly distinguished from *Poo-Lolietum multiflori* (subcluster A2, in which stands are further assembled in subgroups reflecting the two subass. *leucojetosum aestivi* and *brometosum hordeacei*), and *Centaureo-Arrhenatheretum elatioris* (subcluster A3): these two subclusters include less hygrophilous and more nitrophilous stands. Group B gathers the *Molinion* meadows of *Plantagini-Molinietum caeruleae* and *Serratulo-Plantaginetum altissimae*, corresponding to subcluster B1 and B2 respectively. The PCA (Fig. 7) shows the clear separation between *Molinion* and *Arrhenatherion* communities, highlights a strongly intermediate position of *Leucojo-Poetum* between the stands of the two alliances and confirms a greater relationship of *Leucojo-Poetum* with the *Arrhenatherion* coenoses. It also confirms the connection of the Doberdò and Palù meadows with *Leucojo-Poetum*. The multivariate analysis totally agrees with that of Tasinazzo (2009), and the equidistance of *Leucojo-Poetum* from the *Arrhenatheretalia* and *Molinietalia* orders is reconfirmed, also with the addition of the stands from Doberdò and Palù. The analysis confirms the connection of *Leucojo-Poetum* with the *Arrhenatheretalia* communities: therefore, also considering a good expression of *Arrhenatheretalia* and *Arrhenatherion* entities based on syntaxonomic interpretation of species from recent literature (e.g., Biondi and Blasi 2015), it seems preferable to consider *Leucojo-Poetum* as an *Arrhenatherion* association with hygrophilous features tending towards the *Molinion* meadows.

Thanks to the new localities, *Leucojo aestivi-Poetum pratensis* is here validated: it takes an intermediate position between the *Molinion* and the *Arrhenatherion* meadows and shows relevant affinities with *Trifolio-Hordeetalia* coenoses, both in the ecology and floristic structure, recalling the Balkan *Molinio-Hordeion secalini* and the central Apennine *Ranunculion velutini* flooded meadows (see e.g. Pedrotti 1976; Canullo et al. 1988, Venanzoni 1992; Trinajstić 2004; Biondi and Blasi 2015).

*Leucojo-Poetum* encompasses periodically flooded hay meadows that grow on no or lightly fertilised damp soils with high water table gradually drying out in the summer and subject to varying soil moisture conditions, found along the banks of rivers and karstic lakes in the lowlands of NE Italy (upper mesotemperate thermotype). The floristic structure denotes a high value of naturalness: according to Tasinazzo (2009) the community was more widespread in the past, but at present it is very rare due to the agricultural practices based on land reclamation and





**Figure 6.** Cluster analysis of relevés of meadows from NE Italy lowlands (cover data, Chord distance, UPGMA). ■, *Leucojo-Poetum pratensis* (Tasinazzo 2009); ▲, *Poo-Lolietum multiflori leucojetosum aestivi* (Poldini and Oriolo 1995); ▼, *Poo-Lolietum multiflori brometosum hordeacei* (Poldini and Oriolo 1995); ●, *Centaureo-Arrhenatheretum elatioris* (Poldini and Oriolo 1995, rels 1–12); ○, *Plantagini-Molinietum caeruleae* (Marchiori and Sburlino 1982); □, *Serratulo-Plantaginetum altissimae* (Poldini 1989); x, flooded meadow from Doberdò; +, flooded meadow from Palù.

amelioration, and intensive fertilizer use. For further discussion see Tasinazzo (2009).

At Doberdò the community belongs to the uppermost vegetation types dependent on the presence of the lake, along with the dynamically-correlated *Rhamno-Ulmetum minoris* forest and its mantle *Ulmo-Paliuretum spiniae-christi*. It is in catenal contact towards the upper part of the slope with a mesic *Anthoxantho-Brometum* hay meadow, downwards with *Rhamno-Ulmetum* forest and a poplar plantation; in the past it was possibly in contact downwards with *Serratulo-Plantaginetum*, recorded by Poldini (1989) but no longer found.

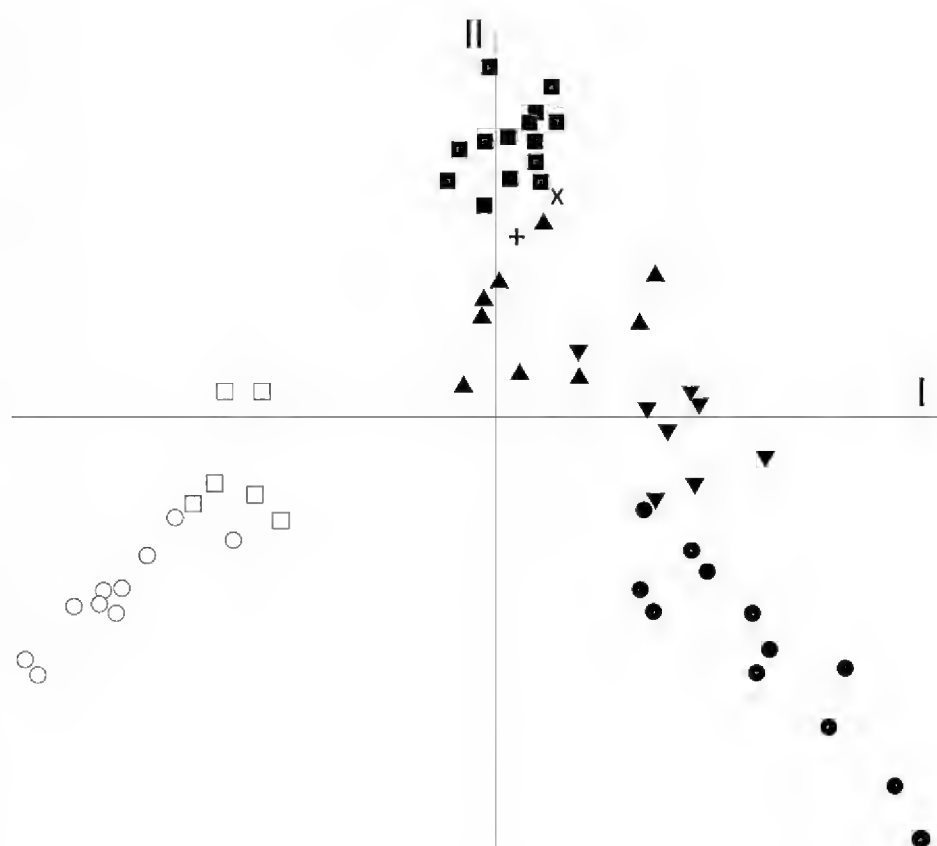
*Annex I Habitat (92/43/EEC Directive): 6510.*

#### **HYGRO-NITROPHILOUS FRINGES WITH MEGA-FORBS (CLASS FILIPENDULO ULMARIAE-CONVOLVULETEA SEPIUM)**

##### **ARISTOLOCHIA CLEMATITIS and VINCETOXICUM HIRUNDINARIA community**

This community includes stands dominated by tall herbs, with the physiognomy determined by the dense cover of *Aristolochia clematitis* and *Vincetoxicum hirsutum* subsp. *laxum*. They are accompanied by various elements of *Agrostietea stoloniferae*, such as *Galium palustre* subsp. *elongatum*, *Ranunculus repens*, *Thalictrum lucidum*. The annual exotic *Bidens frondosa* invades the coenosis during the summer. This thermophilous fringe community is included in the *Calystegion sepium* alli-

ance: it is a hygro-nitrophilous perennial community that grows on damp, silty-clayey, nutrient-rich soils in the lower parts of the lake banks located near the final swallow holes, which are periodically inundated by the raising of



**Figure 7.** PCA of relevés of meadows from NE Italy lowlands (First Component: 14.8 % of total variance, second Component: 11.6 % of total variance). Relevés are labelled as in the dendrogram of Fig. 6.



the water level of the lake at high-water periods. It occurs along the SE, gently sloping bank of the lake, where the water movements tend to accumulate fine mineral particles and organic sediment. In the past this almost flat shore area used to be regularly trampled by livestock. The community is found in contact downward with the *Rorippo-Agrostietum* wet meadow, upward with *Rhamno-Ulmetum minoris*, forming a definitely wet and nitrophilous fringe of this meso-hygrophilous woodland.

*Annex I Habitat (92/43/EEC Directive):* 6430.

*Loc.:* Lake Doberdo, SE bank of the lake, lower part, 5 m a.s.l., 03-06-2015

*Area:* 50 m<sup>2</sup>; *Cover:* 100%; *Number of species:* 14

*Dominant species:* *Aristolochia clematidis* L. (4), *Vincetoxicum hirundinaria* Medik. subsp. *laxum* (Bartl.) Poldini (2);

*Diagnostic species of Calystegion sepium:* *Rubus caesius* L. (+);

*Hygro-nitrophilous species of Agrostietea stoloniferae:* *Agrostis stolonifera* L. subsp. *stolonifera* (+), *Carex hirta* L. (+), *Galium palustre* L. subsp. *elongatum* (C.Presl) Lange (2), *Potentilla reptans* L. (1), *Ranunculus repens* L. (+), *Thalictrum lucidum* L. (1);

*Other species:* *Bidens frondosa* L. (3), *Elymus repens* (L.) Gould subsp. *repens* (+), *Leucojum aestivum* L. (1), *Limniris pseudacorus* (L.) Fuss (+), *Ulmus minor* Mill. subsp. *minor* (pl.) (+).

#### SWAMP WILLOW SHRUBLAND AND WOODLAND (CLASS ALNETEA GLUTINOSAE)

The marsh and hygro-nitrophilous herbaceous communities come in contact with swamp willow scrubs and woods. Along the edges of the main spring pools and brooks, of the main stream, and along the marginal parts of the lake the *Frangulo alni-Salicetum cinereae* scrub (Annex I Habitat (92/43/EEC Directive): -) is spreading as small to large spots. It grows on fine-textured soils that are permanently waterlogged and remain submerged for long periods. *Salix cinerea* is accompanied by *Frangula alnus* and *Salix purpurea*: the occurrence of *S. purpurea*, more linked to riverine habitats, is reported also from the nearby karst Lake Pietrarossa (Poldini 1989) and may be related to the peculiarity of the karst lakes. In the dense willow shrubs few herbs are able to grow, mostly of the class *Phragmito-Magnocaricetea*, such as *Leersia oryzoides*, *Leucojum aestivum*, *Lysimachia vulgaris*, *Limniris pseudacorus*, joined in the summer by *Bidens frondosa* and *Persicaria dubia*.

A peculiar *Salix alba*-wood occurs along the marginal parts of the lake, on hydromorphic soils in areas with a permanently high water table that are frequently and long flooded by regular high water. It is attributed to the swamp association *Galio palustris-Salicetum albae* (Annex I Habitat (92/43/EEC Directive): 91E0\*) recently discussed by Poldini et al. (2020). At Doberdò the physiognomy of the community is given by *Carex elata*, dominant in the herbaceous layer; *Amorpha fruticosa* often appears in the shrub layer (see Poldini et al. 2020). *Frangulo-Salicetum*

*cinereae* may be locally considered the functional mantle of this swamp wood. The community is the most waterward woodland type in contact with marsh communities, notably with *Caricetum elatae*, *Caricetum vesicariae* and reed beds, aquatic communities (*Lemnetea*, *Potametea*) as well as with *Bidentetea* and *Agrostietea* vegetation; landward, it is in contact with the meso-hygrophilous *Rhamno-Ulmetum minoris* woodland.

#### MESO-HYGROPHILOUS WOODLAND AND SHRUBLAND OF THE UPPER BANKS (ALNO-POPULETEA ALBAE, RHAMNO-PRUNETEA CLASSES)

Immediately behind the white willow swamp or the reed- and sedge-beds, a meso-hygrophilous *Ulmus minor*-rich woodland covers the lake banks inundated by seasonal high water. This peculiar lakeshore elm forest, strongly conditioned by the particular hydrodynamics of the Karst wetlands, has been recently described by Poldini et al. (2020) as the new association *Rhamno catharticae-Ulmetum minoris* (Annex I Habitat (92/43/EEC Directive): 91F0), included in the *Dioscoreo-Ulmion minoris* alliance. At Lake Doberdò it occurs with two main aspects, correlated with flooding frequency, length of flooding periods, and water-content of soil. In areas closer to the water, which experience more frequent and prolonged flooding and with high water table, an aspect with abundant *Populus nigra*, often accompanied by *Salix alba*, occurs; the herbaceous layer is characterized by abundant *Leucojum aestivum*, *Aristolochia clematidis*, *Vincetoxicum hirundinaria* subsp. *laxum* and *Galium palustre* subsp. *elongatum*. In the upper parts of the lake margins, inundated only by the highest phases of seasonal high water, *U. minor* joins with *Fraxinus angustifolia* subsp. *oxycarpa* while *Populus nigra* disappears and in the herbaceous layer *Brachypodium sylvaticum*, *Carex sylvatica* and *Viola reichenbachiana* are common. Compared to *Galio-Salicetum*, *Rhamno-Ulmetum* grows on soils flooded less frequently and for shorter periods. It must be highlighted that *Ulmus minor*, a species that is undergoing a decline due to the Dutch elm disease in several areas across Europe, shows a notable vitality and recruitment at Lake Doberdò.

The landward transition between the *Rhamno-Ulmetum* forest and the surrounding xero-thermophilous karst communities occurs through two scrub communities (Annex I Habitat (92/43/EEC Directive): -): a peculiar meso-hygrophilous community with *Paliurus spina-christi* and *Ulmus minor* (always occurring as a shrub) recently formalized as *Ulmo minoris-Paliuretum spinae-christi* by Poldini et al. (2020), which constitutes the landward mantle of *Rhamno-Ulmetum*, and a community with *Prunus spinosa* and *Fraxinus ornus* subsp. *ornus*, found on moist soils probably subject to agricultural uses (livestock) in the past. They represent the outermost situations subject to seasonal inundation and are in catenal contact landward with the karst dry communities *Centaureo cristatae-Chrysopogonetum grylli*, *Pruno mahaleb-Paliuretum spinae-christi*, *Aristolochio luteae-Quercetum pubescentis* and with *Pinus nigra* subsp. *nigra* plantations.



## Other coenoses reported in the literature

Taking into account previous investigations of the plant communities of Lake Doberdò (Vascotto 1967; Poldini 1989) some coenoses were not found in the present study.

The aquatic *Hottonietum palustris* was reported as a rather widespread community in the standing or very slow-flowing waters of the pools and channels in the central-eastern sector of the lake, where *Hottonia palustris* was favoured by the shade provided by the large floating leaves of *Nuphar lutea* and *Nymphaea alba*; in the present study no plants of *Hottonia palustris* were observed throughout the study area. A facies of *Nymphaeetum albo-luteae* with abundant to dominant *Nymphaea alba* was common in the standing or almost standing waters in the same eastern sector, but currently *N. alba* appears to be very rare. Stands of *Persicaria amphibia* aquatic ecophene were present in lentic shallow habitats, often within *Schoenoplectetum lacustris*, and in the western part of the study area a community dominated by *Potamogeton nodosus* was observed in the lower course of the spring brooks, just before their confluence with the main stream; both communities have not been reconfirmed.

Along the eastern banks of the lake, frequently flooded sites with soil remaining damp at low-water periods were colonized by a vegetation dominated by *Eleocharis acicularis*, a typical species of the *Littorelletalia uniflorae* order, arranged in a strip in contact upward with narrow stands of *E. palustris*. In the present study *E. acicularis* has never been found, and these areas are colonized by communities of *Potentillion anserinae* and *Bidention*: this could indicate an eutrophication, and possibly also a change in water regime, resulting in the decline of *E. acicularis* and the spread of hygro-nitrophilous species.

Poldini (1989) recorded a peculiar flooded meadow corresponding to the *Serratulo-Plantaginetum altissimae* association (*Molinion*) spread from Croatia to the Karst area, found on the lake banks subject to periodical flooding and drying out in the summer. The community, characterized by *Plantago altissima*, *Serratula tinctoria*, *Leucjum aestivum*, *Gratiola officinalis*, *Allium angulosum* along with *Phragmito-Magnocaricetea* and *Potentillion anserinae* elements, occurred in contact with *Caricetum elatae* on silty-clayey soils, impacted by livestock trampling. Unfortunately, this valuable community has no longer been found.

## Habitats of conservation interest

In a total area of 35 ha, corresponding to the perimeter of the lake according to the official cartography and approximately to the lake surface at normal water level, 38 coenoses were found: 16 aquatic, 12 marsh, 6 fringing herbaceous and 2 bryophyte coenoses, along with 2 swamp willow communities. Extending the area to the zones liable to seasonal high water (ca. 47 ha), the total number of the plant communities dependent on the pres-

ence of the lake reaches 43 (38 non woody and 5 woody coenoses), adding 3 meso-hygrophilous forest and scrub communities, 1 tall-herb fringe and 1 flooded hay meadow. 21 of the 43 communities are attributed to 8 Annex I habitat types, 1 of which is a priority habitat (91E0\*).

The aquatic associations encompass lowland lentic and lotic communities of (oligo-)meso-eutrophic standing waters and slow-flowing spring brooks and streams, corresponding to habitats 3150 and 3260. The habitat 3150 “Natural eutrophic lakes with *Magnopotamion* or *Hydrocharition*-type vegetation” comprises plant communities found in the permanent pools. The habitat 3260 “Water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation” encompasses almost all the communities found in the moderate- to slow-flowing waters of spring brooks, the main stream and minor channels. In agreement with Lastrucci et al. (2017a), *Ranunculo-Elodeetum nuttallii* was not considered as corresponding to a Natura 2000 habitat, being dominated by an invasive species of Union concern, although the attribution of alien-dominated communities to aquatic habitats of conservation value is currently debated.

The amphibious, small-sized *Cyperus fuscus* vegetation (*Nanocyperion*) colonizing the muddy edges of the main pools is attributed to the habitat 3130 “Oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or of the *Isoëto-Nanojuncetea*”.

The habitat 3270 “Rivers with muddy banks with *Che-nopodium rubri* p.p. and *Bidention* p.p. vegetation” includes the muddy margins of the middle and lower course of the main stream flowing through the polje during the dry periods. These areas may be completely bare in spring or covered by scattered *Phragmito-Magnocaricetea* assemblages, but in summer they are heavily colonized by *Bidention* vegetation; alien annuals represented by *Bidens frondosa*, *B. vulgata* and *Xanthium italicum* are particularly abundant.

The habitat 6430 “Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels” is represented by the peculiar wet and nitrophilous, tall herb fringe with *Aristolochia clematidis* and *Vincetoxicum hirundinaria* that occurs along the lower parts of the lake banks constituting the waterward fringe of the lakeside *Ulmus minor* forest.

The habitat 6510 “Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*)” comprises the periodically flooded *Leucojo aestivi-Poetum pratensis* hay meadow, which depends on seasonal inundations for its existence. The habitat hosts considerable populations of *Leucjum aestivum* and *Viola elatior*. Maintaining regular mowing activities is essential for its conservation.

The lakeshore *Salix alba* swamp (*Galio-Salicetum albae*) can be referred to the priority habitat 91E0\* “Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (*Alno-Padion*, *Alnion incanae*, *Salicion albae*)”, while the meso-hygrophilous *Ulmus minor* forest (*Rhamno-Ulmetum minoris*) is included in the habitat 91F0 “Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*,



*Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers (*Ulmion minoris*)” (Poldini et al. 2020).

It should be remarked that at present the conservation value of many *Phragmito-Magnocaricetea* communities is not properly recognized under the Habitats Directive, and reed and sedge beds have already been proposed as additional habitats to be integrated in Annex I (Peterman and Ssymank 2007; Biondi et al. 2014).

### Proposing Lake Doberdò as a site of priority habitat 3180\* “Turloughs”

According to the Interpretation Manual of European Union Habitats (European Commission 2013), habitat 3180\* encompasses “temporary lakes principally filled by subterranean waters and particular to karstic limestone areas” that annually “fill and empty at particular places”, with a vegetation that “mainly belongs to the alliance *Lolio-Potentillion anserinae* Tx. 1947, but also to the *Caricion davallianae* Klika 1934”, and with the bryophytes *Cinclidotus fontinaloides* and *Fontinalis antipyretica* as characteristic plants. In the strict sense, this habitat type corresponds to the peculiar temporary lakes of Ireland called “turloughs”. Turloughs are shallow depressions in karst areas with a glacial origin that fill seasonally in autumn mostly by groundwater and empty usually in summer through springs, swallow holes and estavelles, drying out for a sufficient length of time during the growing season for their floors to be vegetated by wet grassland or sedge-dominated swards; sometimes they have marsh or permanent open water areas in the centre (Sheehy Skeffington et al. 2006). The lake persists for several months in winter, and there may be sporadic rises at other times of the year in response to high rainfall, with the depth of flooding varying from 0.5 to 6 m; some turloughs dry out completely each summer, others only during dry summers, while others can retain water through the year as channels, pools or small lakes (Sheehy Skeffington et al. 2006; Irvine et al. 2018). They vary in size from less than 1 ha to over 250 ha; most of the turloughs with known size are up to 40 ha (Sheehy Skeffington and Gormally 2007).

Timing, duration and depth of flooding, along with nutrient availability and substrate features are the main drivers of the plant communities variation (Sharkey et al. 2015), but it is difficult to develop generalised models of the vegetation zonation of this highly variable and dynamic habitat: long-flooded areas or permanent pools show features of wetland communities while the less-frequently inundated upper parts of a turlough show a transition to grassland, scrub and woodland; oligotrophic turloughs tend to be dominated by sedges, while those subject to higher nutrient availability tend to be dominated by grasses and herbs (Irvine et al. 2018). In the past, all Irish turloughs were surrounded by woodland, but centuries of grazing have prevented the development of woody species: however, a distinct zonation of the marginal areas can be outlined, consisting of shrubs (*Crataegus monogy-*

*na*, *Prunus spinosa*), and ash, oak and elm forming flooded woods (Sheehy Skeffington 2013). An overview of Irish turlough features is available in Sheehy Skeffington et al. (2006), Sheehy Skeffington and Gormally (2007) and Irvine et al. (2018).

Repeated seasonal transitions between water and terrestrial conditions result in a strongly variable and species-rich ecotone and wetland habitat mosaic: the high value of turloughs for biodiversity conservation is recognized by the EU Habitats Directive, and many are protected as Special Areas of Conservation (Sheehy Skeffington et al. 2006; Irvine et al. 2018). Some turloughs are also designated as Special Protection Areas (SPAs) under the EU Birds Directive (2009/147/EC). Furthermore, turloughs are listed as Groundwater Dependent Terrestrial Ecosystems (GWDTE) under the Water Framework Directive.

These “vanishing lakes” (or “vanishing fields”) are described as virtually unique to Ireland, but similar sites are known from Wales, Spain, Slovenia, eastern Canada (Sheehy Skeffington et al. 2006; Irvine et al. 2018) and other parts of Europe (EUNIS 2020). Indeed, the current definition of a turlough provided by the Working Group on Groundwater (2004), developed to take account that a turlough is an integrated hydro-ecological entity (Tynan et al. 2007), allows a wider interpretation of this habitat type, defined as “a topographic depression in karst which is intermittently inundated on an annual basis, mainly from groundwater, and which has a substrate and/or ecological communities characteristic of wetlands”. Indeed, the habitat 3180\* is an example of Annex I habitat types corresponding to geomorphological units (Bunce et al. 2013). The relationship between turloughs and Ireland is largely a matter of definition (Proctor 2010), and such habitat type should not be confined to a particular country (Sheehy Skeffington and Scott 2008). Actually, according to reports under Article 17 of the Habitats Directive for the periods 2007–2012 and 2013–2018 (EUNIS 2020; Eionet-ETC/BD 2020) the habitat 3180\* includes temporary lakes in karstic regions first described from Ireland but also occurring in Slovenia, Croatia, Estonia, Germany and Wales (in Alpine, Atlantic, Boreal, Continental and Mediterranean biogeographic regions).

Major types of wetlands in the Karst region of Italy and Slovenia are represented by disappearing lakes in poljes and small intermittent lakes, which closely resemble Irish turloughs and in many cases substantially correspond to them (Sheehy Skeffington et al. 2006; Sheehy Skeffington and Scott 2008). The larger wet areas of the Slovenian poljes, such as Cerkljansko polje, Radensko polje and Planinsko polje, have some features different from Irish turloughs: larger size, higher elevation, longer flooding periods, greater depths and small river systems running through and sinking within them; moreover, Irish turlough origin is clearly associated with glaciation (Gunn 2006; Sheehy Skeffington and Scott 2008). However, both the larger wetlands in poljes and many of the small intermittent lakes of the Slovenian karst should be included in the EU Habitats Directive as turloughs (Sheehy Skeff-



ington and Scott 2008), all being unique, valuable karstic areas flooded on a seasonal basis supporting a very high variety of species and communities. Indeed, at present, large wetlands of Slovenian poljes, belonging to the same Dinaric karst system of Lake Doberdò, included in the EU Natura 2000 network are recognized to host the habitat 3180\*, such as the close Lake Cerknica (Cerniško jezero/polje), about 60 km from Lake Doberdò (SAC SI3000232).

Also taking into account the comparison between Irish turloughs and Slovenian wetlands carried out by Sheehy Skeffington and Scott (2008), the major points of affinity of Lake Doberdò with this habitat type can be outlined as follows.

- Lake Doberdò is a wetland that is intermittently inundated on an annual basis mainly from groundwater. It belongs to the karst disappearing lakes associated with a polje, with analogous features to the wet areas of Slovenian poljes. With an area of ca. 35 ha at normal water, its size is comparable to that of most Irish turloughs, and it lies in the lowlands like most Irish turloughs (see Sheehy Skeffington et al. 2006; Sheehy Skeffington and Scott 2008).

- Lake Doberdò meets the criteria proposed by Coxon (1986, 1987a, 1987b) to distinguish turloughs from other wetlands on a hydrological basis: a) seasonal flooding with open water at least 0.5 m deep for part of the year and a dry lake floor for another part of the year (but small residual areas of permanent water may be retained); b) emptying occurs to groundwater via swallow holes or estavelles, with no surface water outlet.

- Like in Irish turloughs, sediments, along with algae films, evidently cover the leaves and stems of the plants of the lake floor (Fig. 3) after flooding, and a thick stripe of dead vegetation occurs around the edge of the lake area.

- The assemblage of plant communities fully agree with the vegetation types reported from Irish turloughs. Turlough vegetation is not unique, including communities of lake margins, fens, marshes or shallow waters: they are mainly grass/forb-dominated, sedge/reed-dominated and aquatic communities, besides shrubland and woodland types found along the margins (O'Connell et al. 1984; Goodwillie 1992). Most communities belong to the alliances *Caricion fuscae* and *Caricion davallianae* (*Scheuchzeria palustris*-*Caricetea nigrae*) and *Potentillion anserinae* (*Agrostietea stoloniferae*), but also to the class *Littorelletea uniflorae* (see Sheehy Skeffington and Scott 2008). Proctor (2010) highlights that the pioneer hydro-nitrophilous communities of *Bidentetea tripartitae* and *Agrostietea stoloniferae*, strictly related to seasonally flooded and nutrient-rich water margins, are particularly associated with turloughs. Irish turloughs are highly variable, due to the great variation of their hydrological regime, substrate and nutrient availability, forming a continuum from oligotrophic to eutrophic, dry to wet sites that cannot be split in clear distinct types (Visser et al. 2006; Waldren 2015): as a result, dominant communities in each wetland can be remarkable different, and between the dry and wet extremes, all possible variation in vegetation organization occur. Wet turloughs are usually charac-

terized by reed, sedge beds, fen and aquatic communities: sedges of *Scheuchzeria palustris*-*Caricetea nigrae* are often common or dominant, but large *Carex elata*-dominated stands of *Magnocaricion* (*Phragmito-Magnocaricetea*) can be found as well (see e.g. Goodwillie 1992; Sarr et al. 2015; Sharkey et al. 2015). Indeed, *Carex elata* is included in the characteristic species of the “tall sedge” community type of turloughs described by Goodwillie (1992), along with *C. acuta*, *C. rostrata* and *C. vesicaria*, and it is listed with *Carex viridula* as the dominant species of the “turlough floor meadow” type in the analysis of the Burren National Park by Sarr et al. (2015). *Schoenoplectus lacustris* and *Phragmites australis* beds have been recorded in a number of turloughs (O'Connell et al. 1984; Goodwillie 1992; Sarr et al. 2015). Various turloughs retain areas of permanent open water that host *Potametea* communities. The range of vegetation types of Lake Doberdò matches that of wet Irish turloughs, such as Skaghard Lough (SAC IE0001926) or Termon Lough (SAC IE0001321) (see Goodwillie 1992; Sarr et al. 2015).

- The floor of Lake Doberdò, especially in the central and eastern parts, is covered by large patches of bryophytes, mainly *Fontinalis antipyretica*, that colonize the muddy spaces among reeds or sedges. *Cinclidotus fontinaloides* covers the rocks of the spring areas, but it is also found growing abundant on the bases and low branches of the surrounding shrubs and trees, in relation to the height of flooding. This bryophyte is considered as a regular indicator of the location of a turlough (e.g., Sheehy Skeffington et al. 2006), and it is the only plant along with *Fontinalis antipyretica* listed as characteristic of the 3180\* habitat in the EU Interpretation Manual (European Commission 2013).

- Like turloughs, Lake Doberdò was in the past a very important area for the economy of the local population; reed and sedge beds were regularly mowed for various uses providing an important source of income, while the meadows that used to cover the marginal parts of the basin were mowed or grazed by livestock. Traditional agricultural land-use, alongside the hydrogeological characteristics, is recognized as an essential factor for maintaining these ecosystems. Along the banks of the lake, land would be divided in often very thin fields, usually separated by low dry-stone walls, radiating from the lake basin, in order to guarantee access to the water for local farmers, like in Irish turloughs (Sheehy Skeffington and Gormally 2007; Sheehy Skeffington 2013).

Major peculiar features of Lake Doberdò resemble those of the other Slovenian sites that have been attributed to habitat 3180\* (included in SI3000171, SI3000231, SI3000232, SI3000256 SACs). Taking into account that this habitat type is already recognized outside Ireland, including Slovenia and Croatia, its occurrence in Italy is conceivable. On the basis of the geomorphological, hydrological and ecological characteristics and the present vegetation study we propose to consider Lake Doberdò as the priority habitat 3180\* “Turloughs” introducing a new Annex I habitat for Italy.



## Conclusions

Lake Doberdò hosts a very rich variety of plant communities as compared to its rather small extent, which supports the high naturalistic value of this wetland. This is also confirmed by the peculiarity of some woody communities and the number of Annex I habitat types. The diversity in aquatic and marsh communities is remarkable, although the observed coenoses have typically a broad general distribution. Nevertheless, it must be stressed that the area allows a good expression of many vegetation types: the extension of *Caricetum elatae* is impressive and not so common in Italy, providing suggestive views with its vast monotony; *Phragmites australis* stands denote good vitality, in spite of the spreading problem of reed die-back in Europe, and the same holds for *Ulmus minor* woodland. The outstanding habitat diversity of the area can be mainly correlated with the particular and highly variable environmental conditions due to the characteristic hydrological regime of the disappearing Karst lake and traditional agricultural land-use.

This vegetation survey fully confirms the very high value and the peculiarity of Lake Doberdò for biodiversity conservation. However, it highlights an ongoing, dangerous process of environmental change due to both natural and human-related causes including modifications of the hydrological regime and the abandonment of traditional farm practices, and claims the need for active conservation interventions for the preservation and the recovery of such a precious temporary flooded natural area, which we propose to recognize, based on the hydrologic and ecological features, as the priority habitat 3180\* “Turloughs”. We think that the particular hydrological features, the resulting ecotonal nature and the impressive value for the conservation of biodiversity of this disappearing lake mirror the fundamental essence of habitat 3180\*, which has as its model the Irish turloughs, and we share the equalisation discussed by Sheehy Skeffington and Scott (2008) of the value and the need of protection of the karst flooded poljes with the Irish turloughs for biodiversity conservation at the European Union level.

## Syntaxonomic scheme

PLATYHYPNIDIO-FONTINALIETEA ANTIPYRETICAE Philippi 1956

*LEPTODICTYETALIA RIPARII* Philippi 1956

**Fontinalion antipyreticae** W. Koch 1936

*Fontinaletum antipyreticae* Kaiser ex Frahm 1971

*Cinclidotion fontinaloidis* Philippi 1956

*Cinclidotetum fontinaloidis* Gams ex v. Hübschmann 1953

LEMNETEA MINORIS O. Bolòs & Masclans 1955

*LEMNETALIA MINORIS* O. Bolòs & Masclans 1955

**Lemnion minoris** O. Bolòs & Masclans 1955

*Lemnetum minoris* Soó 1927

**Lemnion trisulcae** Den Hartog & Segal 1964

*Lemnetum trisulcae* Den Hartog 1963

POTAMETEA PECTINATI Klika in Klika & Novák 1941

*POTAMETALIA PECTINATI* Koch 1926

**Potamion pectinati** (Koch 1926) Libbert 1931

*Potametum lucentis* Hueck 1931

*Potametum pectinati* Carstensen ex Hilbig 1971

*Potametum pusilli* Soó 1927

*Parvopotamo-Zannichellietum palustris* Koch ex Kapp & Sell 1965 *groenlandietosum densae* (Cirujano, Pascual & Velayos 1986) Felzines 2016

*Ranunculo circinati-Myriophylletum spicati* Tomasz. ex Passarge 1982

*Potamo crisp-Myriophylletum verticillati* Soó 1928

*Ranunculo circinati-Elodeetum nuttallii* De Lange in Passarge 1994

**Nymphaeion albae** Oberdorfer 1957

*Nymphaeetum albo-luteae* Nowiński 1928

**Ranunculion aquatilis** Passarge 1964

*Potamo crisp-Ranunculetum trichophylli* Imchenetzky 1926

**Batrachion fluitantis** Neuhäusl 1959

*Potamo perfoliati-Ranunculetum fluitantis* Allorge ex Koch 1926 *groenlandietosum densae* (Imchenetzky 1926) Felzines 2016

*Hippuris vulgaris* f. *fluviatilis* community

*Veronico beccabungae-Callitrichetum stagnalis* Oberdorfer ex Müller 1962

*Ranunculo trichophylli-Callitrichetum polymorphae* Soó 1927

UTRICULARIETALIA MINORIS Den Hartog & Segal 1964

**Ceratophyllion demersi** Den Hartog & Segal ex Passarge 1996

*Ceratophylletum demersi* Corillion 1957

BIDENTETEA TRIPARTITAE Tüxen, Lohmeyer & Preising ex Von Rochow 1951

*BIDENTETALIA TRIPARTITAE* Br.-Bl. & Tüxen ex Klika in Klika & Hadac 1944

**Bidention tripartitae** Nordhagen 1940

*Polygonetum hydropiperis* Passarge 1965

ISOËTO-NANOJUNCETEA Br.-Bl. & Tüxen ex Westhoff, Dijk & Passchier 1946

*NANOCYPERETALIA FLAVESCENTIS* Klika 1935

**Nanocyperion flavescens** Koch ex Libbert 1932

*Cyperus fuscus* community

PHRAGMITO-MAGNOCARICETEA Klika in Klika & Novák 1941

*PHRAGMITETALIA* Koch 1926

**Phragmition communis** Koch 1926

*Schoenoplectetum lacustris* Chouard 1924

*Phragmitetum australis* Savič 1926

*Typhetum latifoliae* Nowiński 1930

*Iridetum pseudacori* Egger ex Brzeg & Wojterska 2001

*Glycerio-Sparganietum neglecti* Koch 1926



*Phalaridetum arundinaceae* Libbert 1931  
*MAGNOCARICETALIA* Pignatti 1953  
**Magnocaricion elatae** Koch 1926  
*Caricetum elatae* Koch 1926  
**Magnocaricion gracilis** Géhu 1961  
*Caricetum vesicariae* Chouard 1924  
*NASTURTIO-GLYCERIETALIA* Pignatti 1953  
**Glycerio-Sparganion** Br.-Bl. & Sissingh in Boer 1942  
*Beruletum erectae* Roll 1938  
*OENANTHETALIA AQUATICAE* Hejný ex Balátová-Tuláčková, Mucina, Ellmauer & Wallnöfer in Grabherr & Mucina 1993  
**Eleocharito palustris-Sagittarion sagittifoliae** Passarge 1964  
*Eleocharitetum palustris* Savič 1926  
*Persicaria amphibia* f. *terrestre* community  
*Leersietum oryzoidis* Eggler 1933

*AGROSTIETEA STOLONIFERAE* Oberdorfer 1983  
*POTENTILLO ANSERINAE-POLYGONETALIA AVICULARIS* Tüxen 1947  
**Potentillion anserinae** Tüxen 1947  
*Gratiola officinalis* community  
*Ranunculetum repentis* Knapp 1946  
*Potentilla reptans* community  
*Rorippo sylvestris-Agrostietum stoloniferae* Oberdorfer & Müller in Müller 1961

*MOLINIO-ARRHENATHERETEA* Tüxen 1937  
*ARRHENATHERETALIA ELATIORIS* Tüxen 1931  
**Arrhenatherion elatioris** Koch 1926  
*Leucojo aestivi-Poetum pratensis* Tasinazzo ex Castello, Poldini & Altobelli ass. nov.

*FILIPENDULO ULMARIAE-CONVOLVULETEA SEPIUM* Géhu & Géhu-Franck 1987  
*CALYSTEGIETALIA SEPIUM* Tüxen ex Mucina 1993  
**Calystegion sepium** Tüxen ex Oberdorfer 1957  
*Aristolochia clematitis* and *Vincetoxicum hirundinaria* community

*ALNETEA GLUTINOSAE* Br.-Bl. & Tüxen ex Westhoff, Dijk & Passchier 1946  
*SALICETALIA AURITAE* Doing ex Westhoff in Westhoff & Den Held 1969  
**Salicion cinereae** Müller & Görs 1958  
*Frangulo alni-Salicetum cinereae* Graebner & Hueck 1931  
*ALNETALIA GLUTINOSAE* Tüxen 1937  
**Alnion glutinosae** Malcuit 1929  
*Galio palustris-Salicetum albae* Rauš 1976

*RHAMNO CATHARTICAE-PRUNETEA SPINOSAE* Rivas Goday & Borja ex Tüxen 1962  
*PRUNETALIA SPINOSAE* Tüxen 1952  
**Berberidion vulgaris** Br.-Bl. 1950  
**Fraxino orni-Berberidenion** Poldini & Vidali 1995  
*Ulmo minoris-Paliuretum spinae-christi* Poldini & Vidali in Poldini, Vidali, Castello & Sburlino 2020

*Prunus spinosa* and *Fraxinus ornus* subsp. *ornus* community (Poldini et al. 2002)

*ALNO GLUTINOSAE-POPULETEA ALBAE* P. Fukarek & Fabijanić 1968  
*POPULETALIA ALBAE* Br.-Bl. ex Tchou 1948  
**Dioscoreo-Ulmion minoris** Poldini & Vidali in Poldini, Sburlino & Vidali 2017  
*Rhamno catharticae-Ulmetum minoris* Poldini, Vidali & Castello in Poldini, Vidali, Castello & Sburlino 2020

Other syntaxa quoted in the text

*Anthoxantho-Brometum erecti* Poldini 1980; *Aristolochio luteae-Quercetum pubescentis* (Horvat 1959) Poldini 2008  
*pistacietosum terebinthi* Wraber (1954) 1960; *Caricetum elatae caricetosum vesicariae* Balátová-Tuláčková 1976; *Caricetum elatae phragmitetosum australis* Gerdol 1988; *Caricion davallianae* Klika 1934; *Caricion fuscae* Koch 1926; *Centaureo carniolicae-Arrhenatheretum elatioris* Oberdorfer 1964 corr. Poldini & Oriolo 1995; *Centaureo cristatae-Chrysopogonetum grylli* Ferlan & Giacomini 1955; *Ceratophyllo demersi-Elodeetum nuttallii* Ciocârlan, Sârbu, Ștefan & Marian 1997; *Eleocharito palustris-Hippuridetum vulgaris* Passarge 1964; *Hottonietum palustris* Tüxen ex Roll 1940; *Lemno-Callitrichetum cophocarpae* Passarge 1992; *Littorelletalia uniflorae* Koch 1926; *Littorelletea uniflorae* Braun-Blanquet & Tüxen ex Westhoff, Dijk & Passchier 1946; *Lolio-Potentillion anserinae* Tüxen 1947; *Molinio-Hordeion secalini* Horvatić 1934; *Myriophyllo verticillati-Hippuridetum vulgaris* Julve & Catteau 2007; *Plantagini altissimae-Molinietum caeruleae* Marchiori & Sburlino 1982; *Poo sylvicolae-Lolietum multiflori* Poldini & Oriolo 1995  
*brometosum hordeacei* Poldini & Oriolo 1995; *Poo sylvicolae-Lolietum multiflori* Poldini & Oriolo 1995  
*leucojetosum aestivi* Poldini & Oriolo 1995; *Pruno mahaleb-Paliuretum spinae-christi* Poldini & Vidali 2002; *Ranunculion velutini* Pedrotti 1976; *Ranunculo-Siëtum erecto-submersi* (Roll 1939) Th. Müller 1962; *Ranunculo trichophylli-Sietum submersi* Müller 1962; *Ranunculo-Zannichellietum palustris* (Philippi 1981) Passarge 1996; *Rorippo-Phalaridetum arundinaceae* Kopecký 1961; *Saturejion subspicatae* (Horvat 1974) Horvatic 1975; *Scheuchzerio palustris-Caricetea nigrae* Tüxen 1937; *Serratulo-Plantaginetum altissimae* Ilijanić 1968; *Sparganio emersi-Potametum pectinati* Hilbig ex Weber 1976; *Sparganio-Potametum interrupti* (Hilbig 1971) Weber 1976; *Teucrio scordii-Menthetum arvensis* J. Duvign. 1986; *Trifolio-Hordeetalia* Horvatić 1963; *Zannichellietum palustris* Lang 1967; *Zannichellion pedicellatae* Schaminée, Lanjouw & Schipper 1990 em. Pott 1992.

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## Appendix - Location and Dates of relevés

Suppl. material 1: Table S1 - Rel. 1: main stream, 01/10/2015; rel. 2: main swallow hole pool, E sector, 13/08/2018; rel. 3: swallow hole pool, NE bank, 12/04/2017; rel. 4: NE part of the lake area, 12/04/2017; rel. 5: spring area, NW sector, 13/07/2017; rel. 6: spring area, NW sector, 27/05/2018.

Suppl. material 1: Table S2 - Rel. 1: main swallow hole pool, E sector, 13/08/2018; rel. 2: central sector of the lake basin, 27/05/2018; rel. 3: brooks of the SW small springs, 27/05/2018; rel. 4: small spring, SW sector, 15/09/2015; rels 5-6: brooks of the NW small springs, 15/09/2015; rel. 7: small pool with clear water, N sector of the lake area, 12/04/2017.

Suppl. material 1: Table S3 - Rel. 1: lower course of the main stream, E sector, 29/04/2015; rel. 2: brook from the main spring pool, NW sector, 15/09/2015; rel. 3: brooks of the SW small springs 14/07/2017; rels 4-6: lower course of the main stream, E sector, 16/06/2017; rel. 7: lower course of the main stream, E sector, 29/05/2015; rel. 8: middle course of the main stream, central sector, 16/06/2017; rels 9-14: lower course of the main stream, E sector, 16/06/2017; rel. 15: main swallow hole pool, E sector, 16/06/2017; rel. 16: middle course of the main stream, central sector, 16/06/2017; rel. 17: main pool in the central-eastern sector of the basin along the lower course of the main stream, 16/06/2017; rel. 18: brook from the main spring pool, NW sector, 15/09/2015; rel. 19: upper course of the main stream, W sector, 16/06/2017; rel. 20: middle course of the main stream, central sector, 16/06/2017; rel. 21: lower course of the main stream, E sector, 01/10/2016; rels 22-23: middle course of the main stream, central sector, 01/10/2016; rel. 24: main pool in the central-eastern sector of the basin, 13/08/2018; rel. 25: main swallow hole pool, E sector, 16/06/2017; rel. 26: main swallow hole pool, E sector, 03/09/2015; rel. 27: upper course of the main stream, W sector, 13/08/2018; rel. 28: little branch to a swallow hole of the middle course of the main stream, 01/10/2015; rel. 29: middle course of the main stream, central sector, 16/06/2017; rel. 30: main spring pool, NW sector, 16/06/2017; rel. 31: final small swallow hole pool, E sector, 03/09/2015; rel. 32: main swallow hole pool, E sector, 16/06/2017; rel. 33: main spring pool, NW sector, 16/06/2017; rel. 34: brooks of the SW small springs, 21/04/2015; rel. 35: main pool in the central-eastern sector of the basin, 01/10/2016; rel. 36: brooks of the NW small springs, 17/05/2016.

Suppl. material 1: Table S4 - Rel. 1: small pool, N sector of the basin, 12/04/2017; rel. 2: main swallow hole pool, E sector, 16/06/2017; rels 3-4: main pool in the central-eastern sector of the basin along the lower course of the main stream, 16/06/2017; rel. 5: main swallow hole pool, E sec-

tor, 03/09/2015; rel. 6: main swallow hole pool, E sector, 16/06/2017.

Suppl. material 1: Table S5 - Rel. 1: brook from the main spring pool, NW sector, 16/06/2017; rel. 2: brook from the SW small springs, 14/07/2017; rel. 3: brook from the main spring pool, NW sector, 16/06/2017; rel. 4: brook from the main spring pool, NW sector, 28/08/2017; rel. 5: small spring, SW sector, 14/07/2017; rel. 6: brook from the NW small springs, 16/06/2017; rel. 7: main spring pool, NW sector, 16/06/2017; rels 8-11: brook from the main spring pool, NW sector, 16/06/2017; rel. 12: upper course of the main stream, W sector, 16/06/2017; rel. 13: brook from a small spring, NW sector, 17/05/2016; rel. 14: brook from SW small springs, 14/07/2017; rel. 15: brook from SW small springs, 27/05/2018; rel. 16: brook from a small spring, NW sector, 17/05/2016.

Suppl. material 1: Table S6 - Rel. 1: main swallow hole pool, E sector, 16/06/17; rel. 2: main spring pool, NW sector, 16/06/17.

Suppl. material 1: Table S7 - Rels 1-3: banks of the middle course of the main stream, central sector, 14/07/2017; rel. 4: banks of the middle course of the main stream, central sector, 18/08/2017; rel. 5: E bank of the lake, 17/09/2015; rel. 6: banks of the middle course of the main stream, central sector, 18/08/2017; rels 7-8: SE bank of the lake, 17/09/2015; rel. 9: NE bank of the lake, 28/09/2015; rel. 10: banks of the main spring pool, NW sector, 28/08/2017; rel. 11: banks of the main swallow hole pool, E sector, 23/08/2018.

Suppl. material 1: Table S8 - Rel. 1: main swallow hole pool, E sector, 14/07/2017; rel. 2: main spring pool, NW sector, 18/08/2017; rels 3-4: central-eastern sector of the basin, 18/08/2017; rel. 5: NE sector of the basin, 13/08/2018; rel. 6: banks of a brook from the main spring pool, NW sector, 23/08/2017; rel. 7: upper course of the main stream, W sector, 23/08/2017; rel. 8: banks of a brook from the main spring pool, NW sector, 23/08/2017; rel. 9: NE sector of the basin, 13/08/2018; rels 10-11: N sector of the lake, 13/08/2018; rel. 12: NW sector of the lake, 18/08/2017; rels 13-14: N sector of the lake, 28/09/2015; rels 15-16: NW sector of the lake, 19/07/2017; rel. 17: banks of a brook from the main spring pool, NW sector, 28/08/2017; rel. 18: banks of the main spring pool, NW sector, 17/05/2016; rel. 19: banks of a small pool, N sector, 12/04/2017; rel. 20: banks of the middle course of the main stream, 28/08/2017; rel. 21: banks of a brook from the main spring pool, NW sector, 14/07/2017; rel. 22: banks of a brook from the main spring pool, NW sector, 15/09/2015; rel. 23: banks of a brook from the SW small springs, 14/07/2017; rel. 24: banks of a brook from the SW small springs, 03/09/2015; rels 25-26: near main spring brooks, SW sector of the lake, 03/07/2017; rel. 27: near main spring brooks, SW sector, 23/08/2017; rel. 28: near the upper course of the main stream, SW sector, 03/07/2017.

Suppl. material 1: Table S9 - Rel. 1: SE sector of the lake, 29/08/2018; rels 2-4: E sector of the lake, 13/08/2018; rel. 5: SE sector of the lake, 01/10/2015; rels 6-8: banks of the



middle course of the main stream, SE sector, 14/07/2017; rel. 9: NE sector, near a swallow hole, 19/07/2017; rels 10-11: SE sector of the lake, 18/08/2017; rel. 12: banks of the middle course of the main stream, SE sector, 14/07/2017; rels 13-14: SW sector of the lake, 03/07/2017; rel. 15: NE sector of the lake, 19/07/2017; rel. 16: banks of a small spring brook, NW sector, 17/05/2016; rel. 17: banks of a brook from the main NW spring pool, 15/09/2015; rel. 18: NE sector, near a swallow hole, 19/07/2017; rel. 19: SW sector of the lake, 03/07/2017; rel. 20: banks of a brook from the main NW spring pool, 14/07/2017; rel. 21: SW sector of the lake, 03/07/2017; rels 22-23: bed of small spring brooks, NW sector, 17/05/2016.

Suppl. material 1: Table S10 - Rel. 1: brook from a small NW spring, 15/09/2015; rels 2-3: banks of the upper course of the main stream, W sector, 03/07/2017; rel. 4: swallow hole, NE sector, 19/07/2017; rels 5-6: banks of the main swallow hole pool, E sector, 03/09/2015; rel. 7: banks of the streams between the two final swallow hole pools, E sector, 18/08/2017; rel. 8: banks of middle course of the main stream, central sector, 16/06/2017; rel. 9: banks of the main swallow hole pool, E sector, 18/08/2017; rel. 10: central sector of the lake, 18/08/2017; rels 11-13: banks of middle course of the main stream, central sector, 18/08/2017; rels 14-15: areas near the middle course of the main stream, central sector, 14/07/2017; rel. 16: banks of middle course of the main stream, central sector, 18/08/2017; rel. 17: lake margins, E sector, 12/10/2015; rels 18-20: areas near the middle course of the main stream, central sector, 18/08/2017; rel. 21: areas near the upper course of the main stream, W sector, 03/07/2017; rels 22-23: areas near the brooks from the main spring pool, NW sector, 03/07/2017; rel. 24: areas near the brooks from the main spring pool, NW sector, 13/08/2018.

Suppl. material 1: Table S11 - Rel. 1: lake margins, NE sector, 18/08/2017; rel. 2: lake margins near the main swallow hole pool, E sector, 18/08/2017; rels 3-4: lake margins near a swallow hole, NE sector, 19/07/2017; rel. 5: lake margins, NE sector, 19/07/2017; rel. 6: lake margins near the main swallow hole pool, E sector, 18/08/2017; rel. 7: lake margins, NE sector, 19/07/2017; rels 8-9: lake margins, SE sector, 29/04/15, 18/08/2017; rel. 10: lake margins near the main swallow hole pool, E sector, 17/09/2015; rel. 11: lake margins, SE sector, 29/04/15, 19/07/2017; rel. 12: lake margins near the main swallow hole pool, E sector, 18/08/2017; rels 13-16: lake margins, SE sector, 18/08/2017; rel. 16: lake margins, NE sector, 19/07/2017.

Suppl. material 1: Table S12 - Rel. 1: Lake Doberdò, North-Eastern bank of the lake (GO), 21/05/2018, L. Poldini & M. Castello; rel. 2: Palù di Settimo, Cinto Caomaggiore (VE), 45°50'36"N 12°47'55"E, 10/05/2012, S. Tasinazzo.

## Supplementary material 1

### Tables S1–S12

Authors: Miris Castello, Livio Poldini, Alfredo Altobelli

Data type: phytosociological tables

Explanation note: Vegetation of the karst Lake Doberdò

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